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PARASITOLOGY

EDITED BY

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OBSERVATIONS ON BRITISH RAT-FLEAS[1].

JULY—OCTOBER, 1911.

THE observations here recorded relate to rat-fleas: (I) in Suffolk and North Essex, and (II) in Cambridgeshire.

(I) The report by Messrs Strickland and Merriman has entailed a great deal of labour. The field work was mainly carried out by Mr Merriman, who, during the extreme heat of summer, was obliged to bicycle many miles, almost daily, to the different localities where the rat-catching was being conducted. It was essential, if reliable results were to be obtained, that the collector should, so to speak, be at the rat-catcher's elbow during the operations. The work of determining the many specimens of fleas collected was, on the other hand, carried out by Mr Strickland, who also shared in the field work when time permitted. The field work commenced on 2nd July, 1911, and ended on 23rd October, 1911.

(II) The report by Mr Strickland and myself upon rat-fleas in Cambridgeshire is very brief, although it took a good deal of time to collect the data upon which it is based.

GEORGE H. F. NUTTALL,
Quick Professor of Biology, Cambridge.

[1] Republished by permission of H.M. Stationery Office from *Forty-first Ann. Rep. of the Local Gov. Board* 1911–12, Supplement containing the Report of the Medical Officer, being Appendix B., No. 6, pp. 336–349 with 3 charts.—*Ed.*

I. REPORT ON RAT-FLEAS IN SUFFOLK AND NORTH ESSEX.

By C. STRICKLAND, M.A., B.C.,
Assistant to the Quick Professor, Cambridge;
and G. MERRIMAN, F.E.S., F.Z.S.,
Student in Medical Entomology, Quick Laboratory, Cambridge.

(With 3 Charts.)

The investigations herewith reported upon were undertaken at the instance of the Local Government Board in connection with an enquiry in relation to rats and plague in East Anglia. We were commissioned to study the rat-fleas in the suspected plague area, determining more especially their species and the numbers in which they occurred.

In India, the evidence brought by the Indian Plague Commission has proved that fleas are the active agents in transmitting plague from rat to rat: the number of fleas which occurs on rats in India bears a direct relation to the plague incidence among these rodents. The established connection between rat plague and human plague incidence and the fact that *Xenopsylla cheopis*, the common Indian rat-flea, readily attacks man have led to the now generally-accepted conclusion that fleas play an important part in the epidemiology of human plague, especially in India.

In England, Martin and Rowland (1910) found that rat plague prevailed chiefly in those parts of Suffolk where fleas were most numerous on rats. They moreover found *B. pestis*-like organisms in the gut of fleas removed from plague rats. We find that British rats are infested mainly by two species of flea, *Ceratophyllus fasciatus* and *Ctenophthalmus agyrtes*, of which the former only has been proved by experiment to be capable of transmitting plague from rat to rat in India. In that country *X. cheopis* is, however, chiefly concerned in the spread of rat plague. Experimental evidence is still wanting to prove that *C. fasciatus* is capable of transmitting plague from rat to rat under the conditions prevailing in England. It is the only species of rat-flea in this country which has been found to attack man readily under experimental conditions; consequently, if evidence is forthcoming that it serves as a vector of *B. pestis* from rat to rat in England this flea would also have to be regarded as a potential transmitter of the plague bacillus from the rat to man.

Methods.

Collecting the fleas from rats. It was necessary for the purpose of our investigation to accompany the official rat-catchers of the Local Government Board into the field so as to obtain an accurate flea-census. Although trapping was extensively used, most of the rats were captured by ferreting their runs. We were obliged to be present when they were killed because as soon as a rat dies the fleas begin to abandon it. It is, therefore, essential that the fleas should be collected immediately upon the death of the host if a true estimate of their number is desired.

The outfit for collecting consisted of:

(*a*) Clean calico bags with string attached.

(*b*) Fine forceps and camel-hair brushes.

(*c*) Small corked tubes containing 50% spirit carried in a box provided with holes for the reception of the tubes.

(*d*) Slips of paper, which were duly numbered in pencil and dropped into each tube, in accordance with the numbers given to the rats.

The rats, immediately upon being killed, were dropped into the bags, which were firmly tied up to prevent fleas from escaping. The bags containing the rats were subsequently placed in tins and a little chloroform was added before closing the lid. The fleas now abandoned their hosts and died after a few minutes, so that they were easily collected upon opening the bag. Fleas from each rat were put into a separate tube for subsequent examination. The method we have described ensured our obtaining an accurate flea-census based upon the numbers and species of fleas found upon each rat.

Determination of the fleas. The fleas found upon the rats were determined by microscopic examination, a Zeiss binocular dissecting microscope being used for the purpose. For examination it is best to render fleas transparent, and this is most conveniently effected by placing them in strong phenol solution, after drawing off the alcohol in which they are preserved. They may require 24 hours to clear, after which they may be transferred for some minutes to clove oil and thence to balsam if permanent mounts are required. The clearing process renders the internal structures of the male and female genital organs visible through the chitinous integument, whilst the external segments, which are also of specific importance, remain clearly visible.

The Rat. All the fleas which we examined came from *Mus decumanus*. It is well known that it is a difficult matter to catch many

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The Rat. All the fleas which we examined came from *Mus decumanus*. It is well known that it is a difficult matter to catch many

say exactly what the clearly-marked seasonal variation in the average number of fleas per rat was due to, whether to the temperature, humidity[1], or to a combination of these. We think the temperature the more important factor, but this point could only be settled by more extended observations.

For the purpose of comparison with our results we have charted the average number of fleas per rat found by Martin and Rowland during November and December, 1910, in the same part of Suffolk, when the temperature and humidity had declined to a still lower point than they had in October, 1911, during our observations.

TABLE I.

No.	District	Comprising	No. of rats examined	Average fleas per rat	Plague Present (+) Absent (−)
1	Nacton ...	Nacton Parish	22	6·5	−
2	Tuddenham ...	Swilland, Witnesham, Culpho, Tuddenham, Akenham, Claydon.	39	6·0	−
3	North Essex ...	Lawford, Ardleigh, Dedham, Langham, Boxted, Great Horksley.	40	5·8	−
4	Tattingstone ...	Tattingstone, Brantham, Wherstead, Belstead.	54	5·3	−
5	Bawdsey ...	Bawdsey, Alderton	30	5·3	+
6	Hollesley ...	Hollesley, Shottisham, Boyton ...	32	5·1	−
7	Sutton ...	Sutton Parish	22	5·0	+
8	Freston-Shotley	Freston, Holbrook, Harkstead, Shotley, Woolverstone, Chelmondistone.	35	4·8	+
9	Rushmere ...	Rushmere Parish	49	4·3	−
10	Bramford ...	Bramford, Hintlesham, Holton, Sproughton, Great and Little Wenham, Capel St Mary	45	3·8	−
11	Kesgrave ...	Brightwell, Kesgrave, Martlesham ...	69	3·7	−
12	Playford ...	Playford Parish	45	3·6	−
13	Felixstowe ...	Walton, Felixstowe...	45	3·2	−
14	Framlingham...	Rendham, Swefling, Parham, Easton, Earl-Soham.	100	3·2	−
15	Newbourne ...	Foxhall, Newbourne, Bucklesham, Purdis Farm, Waldringfield.	34	2·8	+
16	Bentley ..	Bentley, Washbrook, Copdock, East Bergholt.	45	2·7	+
17	West Suffolk ...	Boxford, Assington...	11	2·6	−
18	Melton ...	Melton, Hasketon, Ufford	47	1·9	−
19	Ipswich ...	Ipswich Borough	22	1·6	+
20	Boulge ...	Boulge, Bredfield	30	0·6	−

[1] The Indian Plague Commission, whilst working at Belgaum, India, found that humidity, within certain limits of temperature, played some part in the increase of fleas. This increase occurred a little time after the increase of humidity.

(7) The majority of fleas were found on the hinder parts of the rat, so that primary buboes, when they occur, might be expected to develop chiefly in the groin, on the assumption that fleas served as vectors.

The species of rat-fleas.

With regard to the species of fleas found on rats in the suspected plague area, we shall (I) give a list of the species and their numbers which we found, and (II) our observations upon each species, adding a few notes by other authors on these species.

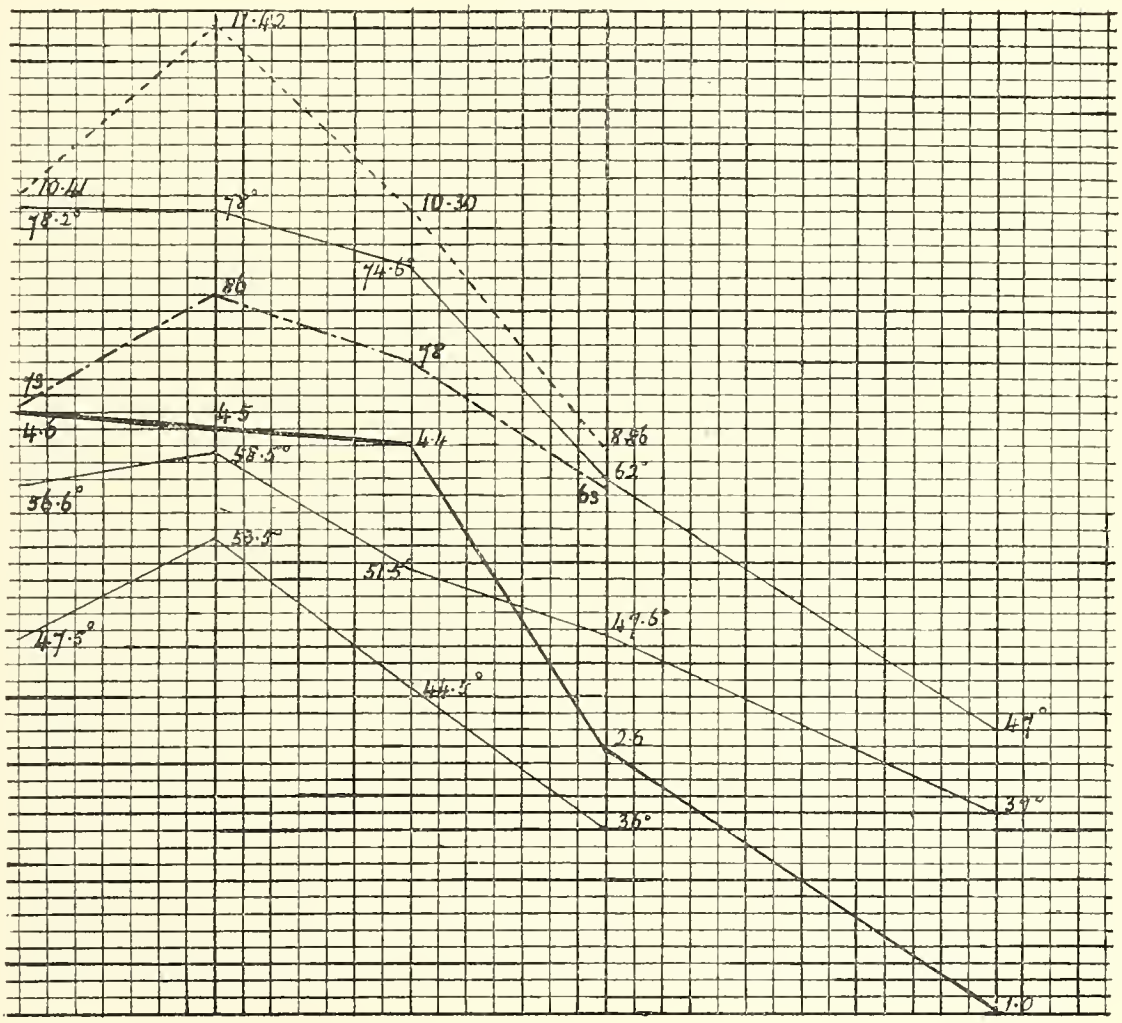

Chart II.

(I) The great majority belonged to two species only. The following table shows the numbers of each species found :

		No. collected
1.	*Ceratophyllus fasciatus*	1986
2.	*Ctenophthalmus agyrtes*	1257
3.	*Ceratophyllus mustelae*[1]	17
4.	*C. walkeri*[1]	8
5.	*Archaeopsylla erinacei*[1]	7
6.	*Ctenophthalmus pentacanthus*[1]	3
7.	*Ctenopsylla musculi*	3
8.	*Pulex irritans*	2
9.	*Hystrichopsylla talpae*	2
10.	*Ctenocephalus canis*	2
11.	*Ctenophthalmus bisoctodentatus*[1] ...	2
12.	*Ceratophyllus gallinae*[1]	1
13.	*C. hirundinis*[1] (?)	1
14.	*Palaeopsylla sorecis*[1]	1
15.	*P. minor*	1
		3293

(II) *Observations made on the various species of fleas found on rats.*

Ceratophyllus fasciatus (*Pulex fasciatus* Bosc d'Antic, 1801), Hilger, 1899.

The number of this species found on grown-up rats recently killed was 1986 from 822 rats—an average of 2·42 per rat.

Besides this, about 70 per cent. of the fleas caught on "nestling" rats were of this species, while of the fleas taken from rats found dead, either of injury or disease, about 90 per cent. were *C. fasciatus*. It would appear from this that *C. fasciatus* deserts a dead rat later than do other species. One of the dead rats was picked up in a yard in which many others lay dead, one of which was subsequently found to have had plague; this rat was infested by 37 fleas, although it was quite cold.

In the various districts mentioned in the table we could find no correlation between the sporadic cases of rat plague and the average number of *C. fasciatus* per rat. In view of the fact that this species bites man, we will here give the average number collected in each district.

[1] Found on *Mus decumanus* for the first time. Rothschild (1910) does not record *Ceratophyllus mustelae*, although Tiraboschi (1904) does so. We have accepted Rothschild's authority in this matter.

TABLE II.

Giving the average number of C. fasciatus *per rat collected in each district.*

	Rat Plague: Present (+) Absent (−)	District
4·4	+	Sutton.
4·2	−	Great Horksley, Boxted, Langham, Dedham, Ardleigh, Lawford.
3·7	+	Alderton, Bawdsey.
3·5	−	Belstead, Wherstead, Tattingstone, Brantham.
3·4	−	Nacton, Levington, Stratton Hall.
3·1	−	Kesgrave, Martlesham, Brightwell.
2·5	+	Foxhall, Purdis Farm, Bucklesham, Newbourne.
2·4	+	Freston, Woolverstone, Holbrook, Chelmondiston, Harkstead, Shotley.
2·4	−	Rushmere.
2·4	−	Playford.
2·1	−	Holton, Capel, Great and Little Wenham, Chattisham, Hintlesham, Sproughton, Burstall, Bramford.
2·0	−	Earl-Soham, Framlingham, Easton, Parham, Gt Glenham, Swefling, Rendham.
1·9	−	Claydon, Akenham, Whitton, Witnesham, Swilland, Culpho, Tuddenham, Westerfield.
1·8	+	Washbrook, Bentley, Great Bergholt.
1·6	−	Hasketon, Melton, Ufford.
1·5	+	Ipswich.
1·3	−	Shottisham, Hollesley, Boyton.
1·0	−	Walton, Felixstowe.
0·3	−	Boulge, Bredfield.
0·2	−	Boxford, Assington.

The seasonal variation of *C. fasciatus* is indicated in Chart I for eight-weekly periods. It dropped from 2·58 per rat to 2·15 as the temperature and humidity fell. Chart III shows the variation per calendar month. There was a *rise* in the average number per rat during September, although the temperature showed a decrease. About 200 rats per month were examined, so that the average given was probably a real one.

Apparently *C. fasciatus* is the most prevalent flea occurring on rats in outhouses, etc., about human habitations, for of those fleas taken from rats caught in these situations 72 per cent. belonged to this species. Yet it appears to hold its own in the country-side, for of the fleas taken from hedgerows, etc., 48 per cent. were of this species. We obtained altogether 1986 specimens of *C. fasciatus*, of which 68 per

cent. came from outhouses, etc., and 32 per cent. from the fields; this is in striking contrast to the other species, 39 per cent. of which came from the buildings and 61 per cent. from the hedgerows. These figures possess a certain practical importance which will be discussed later.

We found *C. fasciatus* on the following hosts:

Host	No. of occasions	No. of individuals
Man	3	4
Stoat	1	1
Mouse	1	2
Ferret	4	121
Rabbit	3	4

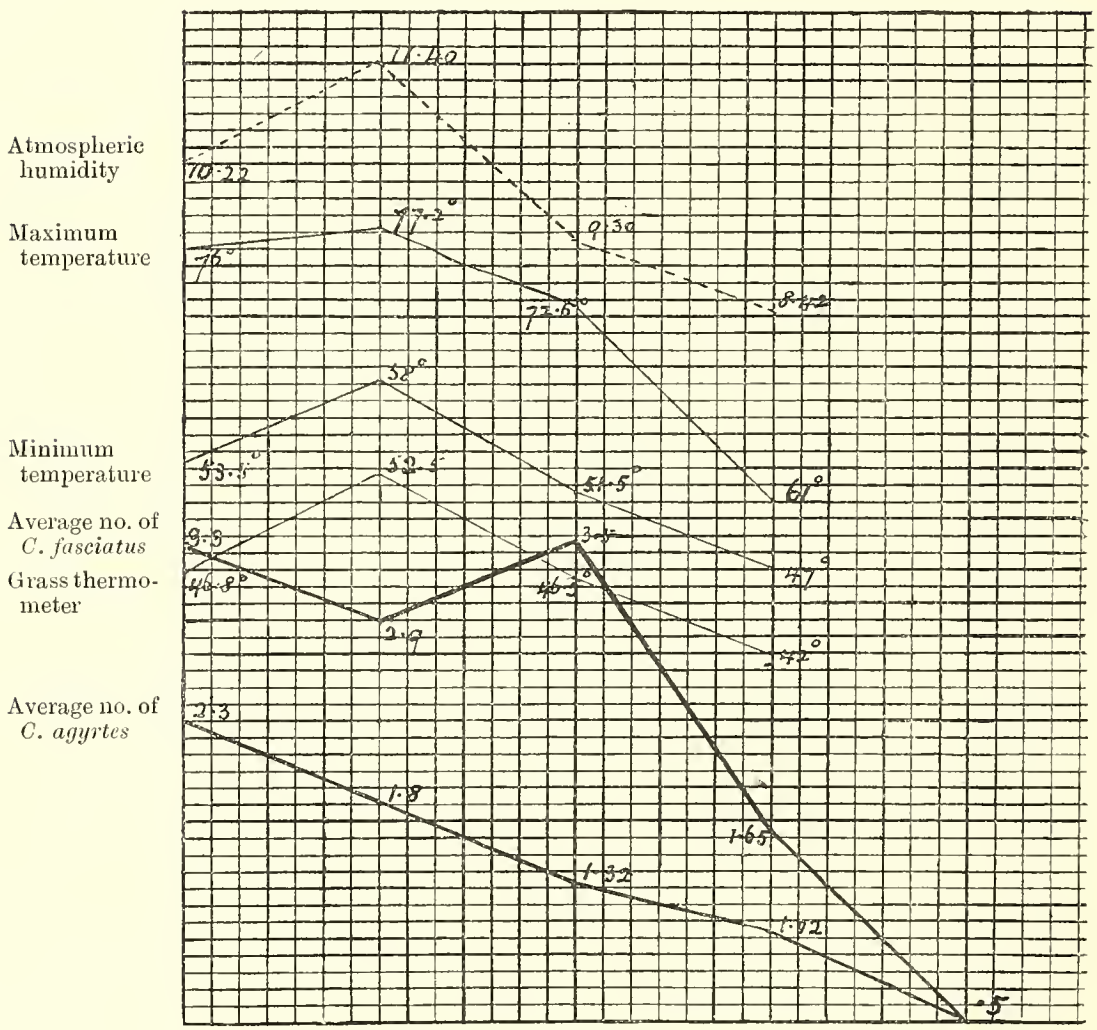

Chart III.

In addition to the above it has been found by other observers on

Mus silvaticus (long-tailed field mouse).
Microtus agrestis (field vole).
Myoxus nitela (garden dormouse).
Myoxus glis (squirrel-tailed dormouse).
Cricetus frumentarius (hamster).
Mustela foina (beech martin).
Mustela putorius (pole-cat).
Crossarchus fasciatus (banded mongoose).
Arvicola savii (vole species).
Pitymys subterraneus.
Canis lagopus (arctic fox).

This species, according to Chick and Martin (1911), and Martin and Rowland (1911), readily bites man; and that is also our experience. It thrives on the rat. One of us (C. S.) has raised it with ease on the rat for two or three years past.

The Indian Plague Commission found that this species in India can transmit plague from rat to rat (*Mus rattus*), two experiments having been successful.

Ctenophthalmus agyrtes (*Typhlopsylla agyrtes* Heller, 1896) Wagner, 1902.

According to Chick and Martin, and Martin and Rowland, this species does not bite man. It was first discovered in fair numbers on rats in Cambridgeshire in 1908 by Nuttall and Strickland, but it nevertheless seems to be widely distributed and nowhere scarce. The rat would, therefore, appear to be a true host for it. With regard to its other hosts, we have taken it from a *stoat* (three specimens) and from a *ferret* (one specimen); while other observers have noted it from the following hosts:

Mus musculus (mouse).
Mus silvaticus (wood mouse).
Evotomys glareolus (bank vole).
Arvicola amphibius (water vole).
Microtus arvalis (continental field vole).
Sorex vulgaris (common shrew).
Crossopus ciliatus (water shrew).
Talpa europaea (mole).
Mustela vulgaris (weasel).
Mustela putorius (pole-cat).

From 822 rats 1257 fleas were taken—an average of about 1·5 per rat. We can find no correlation between the presence of plague in rats

in certain districts and the average number of *C. agyrtes* there any more than we could with *C. fasciatus*. Thirty-five *C. agyrtes* were taken from "nestling" rats (about 30 per cent.), while only five were taken from about 30 rats dead of injury or disease. They may leave their host very rapidly after its death.

The seasonal variation of *C. agyrtes* is shown in Chart I to be apparently dependent on temperature and moisture. In Chart III, however, it is seen that although there is a steady fall from month to month in the average number of fleas per rat, yet the temperature and humidity records do *not* show the same curve. We cannot explain this. We have put in our chart the figures which Martin and Rowland obtained during November, 1910, to show the still further fall in the degree of infestation with *C. agyrtes*.

July, 1911 ...	...	...	2·31 fleas per rat	(154 rats).
August, 1911	...	...	1·80 ,, ,,	(229 ,,).
September, 1911	...	...	1·32 ,, ,,	(202 ,,).
October, 1911	..	...	1·11 ,, ,,	(190 ,,).
November—December, 1910	...		0·5 ,, ,,	(500 ,,).

The proportion of the sexes was slightly lower for the females than in *C. fasciatus*. There were 57 per cent. females and 43 per cent. males for the whole period; and for each month the same proportion, almost exactly, prevailed as in *C. fasciatus*.

C. agyrtes apparently is a "country" flea, for while, in the buildings, only 28 per cent. of the fleas taken were of this species, in the hedgerows 52 per cent. were *C. agyrtes*. Of the total number of *agyrtes*, 61 per cent. came from hedgerows and 39 per cent. from buildings, being the reverse of what was observed in the case of *C. fasciatus*. Martin and Rowland also found a preponderance (about 60 per cent.) of *C. agyrtes* in a lot of fleas taken from rat-nests in hedgerows.

Ceratophyllus mustelae (*Pulex mustelae* Dale, 1878) Wagner, 1898.

We found 17 specimens of this species upon 16 rats in the following parishes:—Playford (2), Bentley (3), Felixstowe (3), Kesgrave (1), Rushmere (2), Brantham (2), Rendham (1), Assington (1), Holbrook (1), Tattingstone (1).

Its common host is the weasel (*Mustela vulgaris*).

Ceratophyllus walkeri Rothschild, 1902.

This species was taken on only eight occasions from as many rats in the parishes of Bentley, Rushmere (3), Tattingstone, Brantham, Lawford, and Felixstowe. On one of the rats it was found in company with *C. mustelae,* both species of flea probably having been picked up from the trail of a weasel.

C. walkeri has also been found on the following hosts :—*Mus musculi, Mustela vulgaris, M. erminea, Sorex vulgaris, Microtus glareolus, M. amphibius, Arvicola sp. M. vulgaris* is, however, considered its true host.

Archaeopsylla erinacei (*Pulex erinacei* Bouché, 1835).

We found *A. erinacei* on two rats, once singly and once six of them, in the parish of Martlesham and the borough of Ipswich. This is the common hedgehog flea. Satunin found it once on *Mus alexandrinus.*

Ctenopsylla musculi (*Pulex musculi* Dugès, 1832).

This, the common mouse flea, was only found three times on rats in East Suffolk. Three specimens were collected : two in Culpho and one in Parham. We found it once on mice in Framlingham and it has also been taken from *Mus silvaticus* and *Mus rattus.*

According to Tiraboschi it does not bite man.

Ctenophthalmus pentacanthus (*Typhlopsylla pentacanthus* Rothschild, 1898) Wagner, 1902.

The true host of this flea is stated to be the field vole, *Microtus agrestis.* It occurs also on *Mus silvaticus, Talpa europaea,* and *Mustela vulgaris.* We have found it on three occasions on *Mus decumanus,* each time singly, in Tuddenham, Walton, and Boxford.

Pulex irritans (*Pulex vulgaris* Linnaeus, 1746) Rothschild, 1908.

The natural host of this flea is *man.* We have found it twice on rats (two specimens) in Rushmere and Playford. Its other hosts are numerous, but according to Rothschild the badger is a true host. A doubt has been expressed with regard to this species serving as a plague vector from man to man, on the ground that the degree of septicaemia occurring in human plague is insufficient to infect the flea.

Hystrichopsylla talpae (*Pulex talpae* Curtis, 1826).

H. talpae was found on two rats caught alive in Dedham and Hollesley, respectively, and on one found dead in Lawford. Its other hosts are as follows:

Microtus arvalis.	*Talpa europaea* (its true host).
,, *agrestis.*	*Sorex araneus.*

Ctenocephalus canis (*Pulex canis* Curtis, 1826–1832).

This species, the common dog flea, was twice found by us on rats in Kesgrave and Tuddenham. Three specimens were caught on a dog at Holton. Its other hosts are *Otocyon megalotis, Canis lagopus, Nasua solitaria* and *Felis jaguarondi*; and it has been found in the nest of the great tit, *Parus major*.

Ctenophthalmus bisoctodentatus (Kolenati, 1862).

Two specimens of this species were found by us on rats in Great Horksley and Bentley, whilst two others were taken from a rat in Hollesley.

Ceratophyllus gallinae (*Pulex gallinae* Schrank, 1804) Rothschild, 1900.

This is the flea which infests fowl and poultry runs. It readily attacks man—a fact well-known in the country. Its normal host must, however, be considered to be the domestic fowl; but its tastes seem to be catholic, as it is found in the nests of many species of birds. In Cambridge, for instance, we have found it in a number of tits' nests (*Parus major*). It has also been taken from the bat (*Vesperugo noctula*) and from the field mouse (*Mus silvaticus*), but it has not, hitherto, been found on the rat. This is evidence that the rat cannot be regarded with favour by this flea, for the two must often be brought into contact in the farm-yard. Indeed, we have caught a batch of rats (Holton) in a barn literally swarming with *C. gallinae*, but they did not harbour a single flea of this species. Only on two occasions did we find this flea upon rats: once upon a rat caught alive in Rushmere and once upon a rat found dead in Bentley. We have taken it several times from man in large numbers, also from the dog once (at Holton), and, finally, from barns and the hole of an old oak tree.

Ceratophyllus hirundinis (Curtis, 1832) Rothschild, 1900.

This species is represented in our collection by a headless specimen. It has only been found previously on sand-martins and swallows (*H. urbica* and *H. rustica*).

Palaeopsylla sorecis (*Ctenophthalmus sorecis* Dale, 1878) Dampf, 1910.

This species was taken once from a rat in the parish of Swefling.

Palaeopsylla minor (*Ceratophyllus minor*), Dampf, 1910.

We have captured this flea once on *Mus decumanus* and once on the stoat. It has previously been taken from *Mustela putorius*.

Species of fleas found on other hosts than rats[1].

The species of fleas referred to in the foregoing pages have been found by us to occur on the following hosts other than rats:

Man	...	*Pulex irritans*, *C. gallinae*, *C. agyrtes*, *C. fasciatus*.
Stoat	...	*P. minor*, *C. agyrtes*, *C. fasciatus*.
Mouse	...	*C. musculi*, *C. fasciatus*.
Dog	...	*C. canis*, *C. gallinae*.
Ferret	...	*C. fasciatus*, *C. agyrtes*.
Rabbit	...	*C. fasciatus*, *C. agyrtes*, *Spilopsyllus cuniculi*[2].
Hedgehog	...	*C. erinacei*.

From the point of view of their numbers only, *C. fasciatus* and *C. agyrtes* appear to be the only two species which could have any practical significance in the epidemiology of plague, yet the other species which we found might become important another year or under other conditions. A species rare one year may become dominant another. For instance, Tiraboschi, Verjbitski, Gautier and Raybaud, and Tidswell have all reported on the great prevalence of *Ctenopsylla musculi*, but we only collected three specimens of this species.

[1] Fleas were also found in the following situations away from any host:

Barn	...	*C. gallinae*.
Hole of tree	...	*C. gallinae*.
Rats' nests	...	*C. fasciatus*, *C. agyrtes*.

[2] *Spilopsyllus cuniculi* (*Pulex cuniculi* Dale 1878). This species has been previously found on the rabbit, cat, and rat. We obtained one specimen from a rabbit but *none from the rat*. Martin and Rowland state that it bites man.

The species of fleas, granted they are numerous enough, are only important if they bite hosts susceptible to plague infection, and so are able to transmit the disease from one to another of these hosts.

Of the species which we found on rats all, with the exception of *C. fasciatus* and *C. agyrtes*, had perhaps only an accidental connection with the rats, and possibly never bite the rat; we cannot, however, give certain evidence of this. Of the species which we rarely found on the rat, *C. musculi* and *S. cuniculi* are the common mouse and rabbit flea respectively, and as the mouse and rabbit are subject to epizootics of plague these fleas probably serve as vectors of the bacillus. *S. cuniculi* is said to bite man, in which case plague among rabbits becomes directly dangerous to man. Plague among mice must be transmitted to rats or other hosts by the agency of a flea common to the two species in order to be dangerous to man.

C. fasciatus, being parasitic on the mouse and rabbit, may sometimes be the cause of the transmission of the disease between these hosts.

C. agyrtes, in view of its numbers, is the next most important species, but it does not bite man. The significance, therefore, is restricted to the possibility of its transmitting and keeping up plague from rat to rat.

Other ecto-parasites of rats.

It is not probable that ecto-parasites of rats, other than fleas, have any significance in the epidemiology of plague; but we may here mention those which we found:

Acarina were the most abundant of other ecto-parasites, occurring on about 100 rats. There were one or two Coleoptera, and a very few Anopleura (lice). We did not find more than five rats with lice out of many hundreds examined[1].

Ticks. Three female specimens of *Ixodes tenuirostris* from two rats; found for the first time on rats, their usual hosts in this country being small mammals (shrews, harvest mice, voles). (Determined by G. H. F. Nuttall.)

Other Mites. Mostly *Haemogamasus hirsutus*, the common species found in moles' nests; *Gamasus coleoptratorum; Gamasus terribilis; Gamasus* sp.? nymph. (Determined by N. D. F. Pearce.) *Notoedres* sp., the cause of ear-scabies.

Anopleura. Haematopinus spinulosus; Haematopinus sp.?

[1] As many of the rats were found by Drs MacAlister and Brooks to be infected with *Trypanosoma lewisi*, it is interesting to note the scarcity of lice, as these are credited by some authors to be the usual carriers of the trypanosomes.

Summary.

To summarize our principal observations made in the course of the investigation into the rat-fleas of the suspected plague area of East Suffolk, July—October, 1911:

(1) We found an average of four fleas per rat: 822 rats were examined and 3293 fleas taken.

(2) The average was subject to a local variation (0·6 to 6·5).

(3) 15 species of fleas were taken from the rats, but of these there were only two species, *C. fasciatus* and *C. agyrtes*, which occurred in any numbers.

There were *C. fasciatus* 1986 or about 60 per cent.
C. agyrtes 1257 „ 38 „
Rare species 50 „ 2 „

(4) The average number of fleas per rat and the percentage of rats infested by fleas showed a well-marked seasonal variation, there being a considerable decline in the numbers as the cooler weather came on. *Ceratophyllus fasciatus* and *Ctenophthalmus agyrtes* both participated in a similar way in this variation.

(5) *C. fasciatus* is chiefly found on rats caught near human habitations; *C. agyrtes* on those caught in the hedgerows.

In conclusion, we wish to tender our best thanks to all those gentlemen who have helped us in our work. Prof. G. H. F. Nuttall, F.R.S., very kindly aided us in organising the work and in the revision of our manuscript; Dr A. Eastwood, on behalf of the Local Government Board, placed at our disposal the material upon which we made our observations; Dr A. Pringle, Medical Officer of Health for Ipswich, kindly supplied us with the meteorological records of that town; Mr C. J. Huddart, in his administrative capacity, gave us much assistance; and the Hon. N. Charles Rothschild confirmed some of our determinations.

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II. REPORT ON RAT-FLEAS IN CAMBRIDGESHIRE.

By GEORGE H. F. NUTTALL, F.R.S.,
and C. STRICKLAND, M.A.

The following record relates to fleas collected from rats in and about Cambridge during the period 3rd March, 1909, to 20th November, 1911. We had difficulty in obtaining rats in Cambridge during the year 1911 owing largely to the high price asked by professional rat-catchers who usually sell them for sporting purposes. We have, consequently, included data collected by us during the two years before this investigation was undertaken on behalf of the Local Government Board.

With regard to the species of fleas collected from the rats, by far the larger numbers were *C. agyrtes*, especially in the case of the rats captured at Cherryhinton Brook. A few *C. fasciatus* and but one specimen each of *P. irritans* and *C. bisoctodentatus* were found on the rats. The largest numbers of fleas per rat (*C. agyrtes*) were captured in February and March.

		Locality	No. of rats examined	No. of fleas collected	Average No. of fleas per rat
1909:	March 3	Cherryhinton Brook	2	5	2·5
	,, 9	,,	27	54	2·
	,, 18	,,	1	5	5·
	,, 19	,,	1	33	33·
	April 29	,,	4	3	0·7
	May 11	,,	3	3	1·
	June 7	,,	3	2	0·6
	,, 12	,,	2	10	5·
	,, 22	,,	6	11	1·8
	July 6	,,	5	2	0·4
	August 3	,,	1	3	3·
	,, 24	Chesterton ...	3	1	0·3
	,, 31	Cherryhinton Brook	2	2	1·
	September 8	,,	1	2	2·
	,, 11	,,	2	12	6·
	October 12	,,	5	9	1·8
	,, 29	,,	3	7	2·3
	November 10	,,	4	5	1·2
	,, 28	,,	9	18	2·
	December 15	Comberton ...	11	5	0·4
1910:	February 7	Cherryhinton Brook	2	23	12·5
	,, 28	,,	2	2	1·
	March 9	,,	1	15	15·
	,, 22	,,	4	12	3·
	June 21	,,	2	5	2·5
	August 15	,,	4	12	3·
	November 14	,,	3	3	1·
1911:	February 15	,,	6	9	1·5
	,, 28	,,	3	5	1·6
	October 28	,,	1	5	5·
	September 15	Chesterton ...	5	6	1·2
	November 12	Milton Road ..	10	4	0·4
	,, 20	Wilbraham ...	12	4	0·3
		Totals	150	297	2·

THE ANATOMY OF *ARGAS PERSICUS* (OKEN 1818).

PART I.

By L. E. ROBINSON, A.R.C.Sc. Lond.,
and J. DAVIDSON, M.Sc. Liverpool.

(*From the Cooper Laboratory for Economic Research, Watford.*)

(With Plates I to VI and 2 Text-figures.)

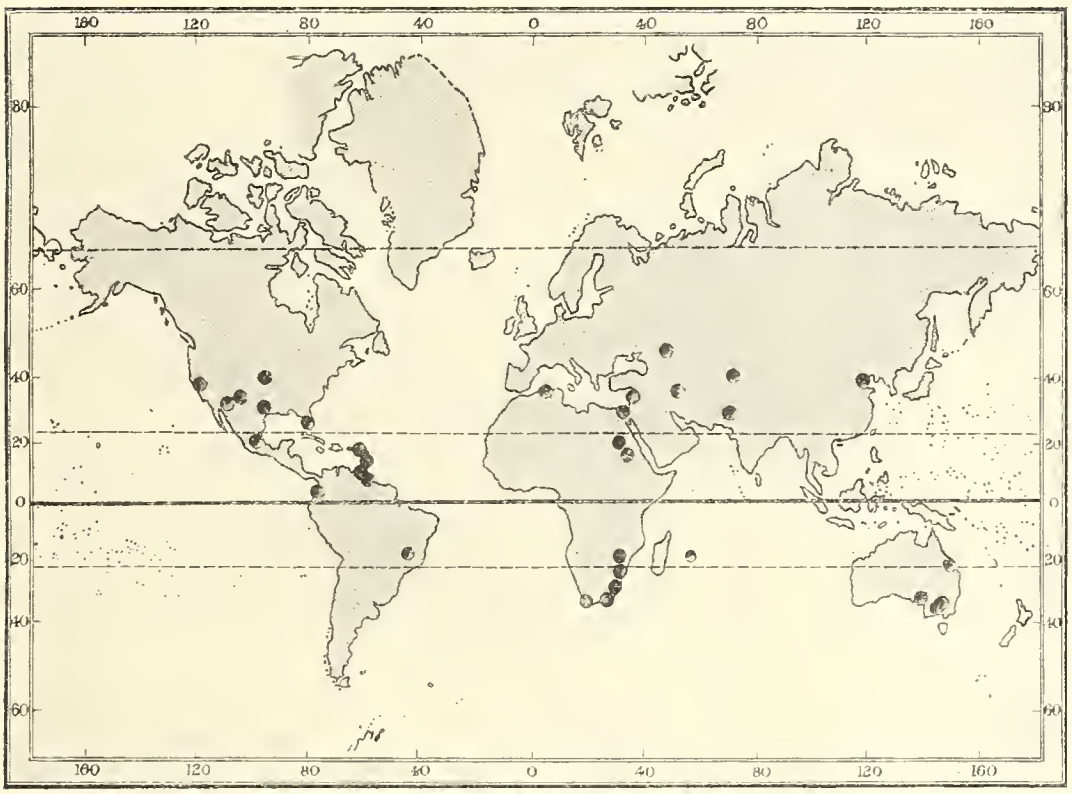
Introduction.

The importance of the *Argasidae*, in relation to the transmission of disease, has suggested the need of a moderately detailed description of the anatomy of an example of the family. With the object of supplying this want, the authors have made a study of a widely distributed species —*Argas persicus*—and they venture to hope that the work embodied in the following pages will furnish something towards the much-needed information, the present lack of which adds to the many difficulties which are encountered in investigations concerning the life-stages of pathogenic *Haematozoa*.

That *Argas persicus* plays a rôle in the transmission of *Spirochaetosis* of domesticated birds is now common knowledge. Apart from this association, however, this tick is one of the most troublesome pests which affect poultry, killing enormous numbers of birds from the loss of blood and the "tick-worry" consequent upon its bites.

The species has a remarkably wide range of distribution. From the map (Text-fig. 1) it is seen that in practically all the countries lying between the fortieth parallels of north and south latitude *Argas persicus* is known to exist, and there is little doubt that, as time goes on, new records of its occurrence will fill many of the empty spaces

which are scattered over this zone. The indiscriminate transportation of poultry is, without question, the explanation of this world-wide dispersion of the species. Its original fatherland is more than doubtful. The specific name "persicus" is accounted for by the fact that the earliest accounts of the species are derived from the writings of Europeans who made a temporary residence or travelled in Persia, in the second decade of the nineteenth century[1]; yet it is very questionable to suppose that Persia is the original source from which the species has been disseminated. The far-reaching invasions of the ancient Persians



Text-fig. 1.

took them to many countries in which *Argas persicus* now prevails; and, in consequence, there is as great a probability that the tick was imported into Persia, as there is for the assumption that it is an indigenous species.

The economics of the species have been the subject of many contributions to the literature, the majority of which deal principally with

[1] See Oken (1818), also Fischer de Waldheim (1823), and Laboulbène, A., and Mégnin, P. (1882).

the life-history and habits, some including a more or less detailed description of the external structures. The only published paper dealing specially with the anatomy of *Argas persicus* is that of Heller (1858), a lengthy dissertation with four plates of twenty-five figures, to which further references will be made.

The synonymy, iconography, geographical distribution, hosts, general biology and systematic position of the species are treated extensively in a recently published monograph, to which the reader is referred[1].

Technique.

The greater part of the material used in this work was sent from South Africa by Mr C. P. Lounsbury, of Cape Town, to whom the authors express their most grateful acknowledgements. Their best thanks are also due to Prof. G. H. F. Nuttall, of Cambridge, for material collected at Kasauli, Punjab, India, and to Mr J. D. Davidson who collected and sent supplies from Potchefstroom, Transvaal, S. Africa. In addition to these sources, the authors were able to avail themselves of the store of preserved material in the Cooper Collection, Watford, which included specimens from Africa (Algeria and Rhodesia), from Texas, U.S.A., and from Queensland, Australia.

In the study of the external anatomy, the same methods were used as those which have been described in an earlier communication to this Journal, in which one of the authors (L. E. R.) collaborated[2].

For the general examination of the external structures, living specimens may be killed by a *momentary* immersion in boiling water. Apart from its simplicity, this method has two advantages—the specimen dies with the appendages in a state of extension—and the adherent dirt, which frequently obscures the surface details, is for the most part removed. If it is desired to make a cleared and mounted preparation of such a specimen, the careful application of a little soap and warm water on a small camel-hair brush is advisable, as the neglect of this precaution frequently spoils an otherwise good preparation. The clearing of a specimen is best effected with an aqueous solution of potash (10 %) which should always be used cold; if, with the object of hastening the operation, heat is applied, the chitin swells and many of the finer details are irretrievably lost.

In making preparations of the cuticle, it is advisable to remove and

[1] Nuttall, G. H. F., Warburton, C., Cooper, W. F. and Robinson, L. E. (1908).
[2] Nuttall, G. H. F., Cooper, W. F. and Robinson, L. E. (1908).

mount the integument of the dorsal and of the ventral surfaces separately. This is comparatively easy in the case of *Argas persicus*. At the line of junction between the dorsal and ventral marginal scutellae, the cuticle splits quite readily, and by inserting a fine needle obliquely under the skin, and passing it round the entire margin of the body, the two surfaces are separated and may then be removed by lifting the posterior margin with a pair of fine forceps, the muscular attachments being broken down progressively with the needle, as the cuticle is gradually and gently drawn forward. The two surfaces come away practically clean, any adherent tags of muscle being easily removed with the fine forceps, and an immersion of short duration in the potash solution is then sufficient to remove the soft parts of the capitulum and legs. Such preparations may be stained before mounting in Canada balsam, with picric acid in xylene, fuchsine, Bismarck brown or other stains, but this operation is really unnecessary if the preparations have not received excessive treatment in the potash solution. The photomicrographs which illustrate the structure of the cuticle (see Pl. II, figs. 3 and 4) were prepared in the manner described above, and despite the fact that they are unstained, the details of the cuticular surface are faithfully rendered in the reproduction.

In the study of minute parts, as the digit of the chelicera for example, preparations mounted in glycerine, glycerine jelly, Farrant's medium, or monobromide of naphthalene, are useful adjuncts to the balsam mounts.

It is very necessary to check all observations made on cleared, transparent specimens, wherever possible, by examination of the same structure as an *opaque* object. The risk of misinterpretation of the appearances presented by cleared specimens, mounted in highly refractive media, is enormous; and observations made on such specimens are a fertile source of the errors which have appeared from time to time in the published literature.

Serial sections are indispensable if it is desired to form a complete idea of the structure of such a part as the capitulum of the tick. The technique which the authors have used for the preparation of serial sections of *Argas persicus* will be fully described in the second part of this paper, but it will not be out of place to indicate the main principles now.

Satisfactory fixation of the tissues is by no means easy to ensure in the case of Arthropods possessing a stout, highly chitinised integument. For the study of the chitinous parts and the general anatomy, provided

that faithful preservation of histological detail is not a *sine qua non*, the classic Kleinenberg's picro-sulphuric acid fixative, used undiluted and hot, gives good results. After fixing, every trace of the fixing reagent must be eliminated from the tissues, prior to embedding in paraffin. Perfect dehydration is essential to successful embedding, and the absolute alcohol-chloroform-paraffin sequence—the *Senkmethode* of F. E. Schulze[1]—has proved of admirable service in the hands of the authors. Hard paraffin with a melting-point of 58° C.–60° C. should be used, and the duration of the paraffin bath must not be prolonged for a moment more than is absolutely necessary. If the vacuum method of embedding can be applied, the time required for thorough penetration by the paraffin is very materially reduced. A little ingenuity will suggest a method by means of which an ordinary mechanical air-pump, such as is available in most laboratories, can be utilised for the purpose, and the results will prove to be as good as those obtained by the use of the expensive, vacuum-embedding baths which are advertised in the instrument-makers' catalogues.

Tick material, prepared by the methods described above, will cut perfectly on a microtome of the Minot pattern, without displacement or fracture of the chitinous parts. A thickness of 10 μ is most suitable for general purposes. It is perhaps unnecessary to observe that the microtome knife should be in perfect condition to ensure successful results.

The authors have tried the collodion-method of embedding, but the results were far from satisfactory. With proper care, the paraffin method yields results which are all that can be desired.

The preparation of material for the study of the histological details of the internal organs involves more care. Kleinenberg's fixative is quite unsuitable; Carnoy's fluid, Flemming's fluid, or others which give a satisfactory fixation of the soft tissues must be used. It has been found necessary to aid the penetration of these fluids by the use of an injecting syringe, in the manner advocated by Nordenskiöld[2]. The description of these special methods will, however, be more conveniently dealt with in connection with the internal anatomy.

[1] Rawitz, B., *Leitfaden für histiologische Untersuchungen*, Verl. Gustav Fischer, Jena, 1895, p. 33.

[2] Nordenskiöld, E. (1908).

External Anatomy.

Plates I and II.

In general structure, *Argas persicus* is a typical example of the family *Argasidae*. As in the majority of the *Acarina*, the opisthosoma[1] of the adult and nymphal stages exhibits no obvious external traces of the primitive segmentation, and even in the larva, the arrangement of the hairs on the surfaces of the body is such as to give only the merest suggestion of metamerism.

The contour of the body (Pl. I, figs. 1 and 2) is oval, narrowing anteriorly, the maximum width being attained at about the level of the posterior third of the entire length. The dorsal surface of unfed individuals is flattened, and towards the periphery, where the thickness of the body thins out to an acute margin, is usually somewhat reflexed. The ventral surface is always more or less convex.

In fasting specimens, the prevailing colour of the dorsum is a dull greyish yellow, darker and opaque in the median field, paler and translucent towards the margins. The ventral surface, legs and capitulum are always paler in colour than the dorsum. After feeding, the general colour alters, gorged specimens presenting a somewhat dark, leaden appearance, due to the ingested blood showing through the translucent integument. The legs and capitulum, however, retain their pale colour and show in stronger contrast. Both surfaces of the body then become strongly convex, and in a fully distended individual, the margin loses its acuteness. In partially gorged young individuals, and also specimens in which the contents of the alimentary canal have been absorbed, it is possible to define the form of the stomach with its coecal appendages through the dorsal body wall (see Pl. I, fig. 1, *st.* and *cc.al.*). In the latter case, the alimentary canal retains a dark-coloured residue of undigested detritus which makes it clearly visible.

The body is covered with a stout, chitinous cuticle of a leathery texture. The greater part of the surface is rough and granular, excepting the capitulum with its appendages, the legs, and certain parts of the body to be specified later.

Scattered over the entire dorsal surface, but confined to the posterior and marginal parts of the ventral surface, are a large number of minute dark-brown glistening areas with a more or less circular outline. These areas, which we term *discs* (see Pls. I and II, figs. 1–4, *dc.*), have

[1] Lankester, E. R. (1904).

attracted the notice of the majority of observers of this species. They are disposed in a regular conformation, but there is frequently some slight asymmetry of arrangement between the right and left halves of the body. These discs, as was first observed by Heller (1858), mark the sites of insertion of the body-muscles and are strictly homologous with the grooves which form a conspicuous feature of the superficial anatomy of the *Ixodidae*. They are quite visible to the naked eye, particularly in gorged individuals, where, owing to the distension of the body, they appear as deep pit-like depressions, the attached muscles having prevented the expansion of the body at these points.

Towards the anterior extremity of the ventral surface, snugly ensconced in a deep depression termed the *camerostome* (*cam.*), is the *capitulum* (*cap.*). The capitulum is comprised of a basal portion—the *basis capituli* (see Pl. IV, fig. 8, *b.c.*), upon which are borne the first and second pairs of appendages—the *chelicerae* and the *palps* (*ch.* and *p.*). The oral opening is situated on the capitulum but is concealed from the ventral aspect by the *hypostome* (*h.*)—a median prolongation of the basis capituli. The chelicerae are situated above, and the palps on either side of the mouth. The proximal portion of the basis capituli is partially telescoped into a large, obliquely inclined opening, the *capitular foramen*, in the ventral body wall, and is articulated with the body in such a manner as to allow free movement in the sagittal plane. In the resting state, the capitulum is maintained in a position of extension, being depressed into the cavity of the camerostome.

The camerostome (see Pl. III, fig. 7, *cam.*) is approximately rectangular in shape, and its lateral walls are raised into a pair of salient integumental folds, the *camerostomal folds* (*cam.f.*) which originate some distance posterior to the basis capituli. These camerostomal folds protect the retracted capitulum, on either side of which they run forwards, to terminate at the antero-lateral angles of the camerostome.

The four pairs of legs (*l. i*, *ii*, *iii* and *iv*) are situated on the anterior half of the ventral surface, the *coxae* of the 1st pair lying immediately external to the posterior half of the camerostomal folds. With the exception of a narrow interspace between the 1st and 2nd pairs, all the coxae are contiguous. They are firmly articulated to the ventral body wall, but are capable of a certain amount of movement—abduction and adduction. This mobility of the coxae is rendered possible by the fact that the body wall is raised into two prominent longitudinal folds. The outer or *supracoxal fold* (*s.cx.f.*) runs along the external margins of the coxae, curving inwards in front of coxa I, and merges into the

general plane of the ventral surface just anterior to the antero-lateral angles of the camerostome. At the level of the last pair of coxae, the supracoxal folds diverge somewhat abruptly and, after a short outwardly curving course, terminate near the lateral margin of the body about the level of the posterior fourth of the body length. The inner or *coxal folds* (*cx.f.*) run along the mesial margins of coxae I, II and III. They terminate anteriorly at the interspace between coxae I and II. Like the supracoxal folds, the coxal folds diverge at the level of coxa IV, and terminate near the anterior limit of the posterior third of the body.

These integumental folds are always clearly defined and are most conspicuous in old starving specimens. Engorgement tends to obliterate the terminal portions of the folds.

In addition to the buccal orifice, already alluded to, the natural openings on the surface of the body, common to both sexes of the adult stage, are two median, unpaired openings—the *genital aperture* (*gen.ap.*) and the *anus* (*an.*). In addition to these, a pair of *spiracles* (*sp.*) and the two orifices of the ducts of the *coxal glands* (see Pl. III, fig. 7, *o.cx. gl.*) open on the ventral surface. The female possesses yet another aperture, viz. the mouth of the ovipositing organ, which, in deference to its original describer, Nuttall (1908) has termed *Gené's organ* (see Pl. III, fig. 7, *o.Gen.org.*). This aperture is situated in the camerostome, immediately anterior to the fold formed by the union of the basis capituli with the roof of the camerostome.

The genital aperture appears in both sexes as a transversely placed, ventral opening, situated in the median line, some little distance posterior to the basis capituli, opposite the interspace between the first and second pairs of coxae. In the second nymphal stage (*deuteronymph*) a small imperforate pit, the *Anlage* of the future genital aperture, is to be found in the same position.

The anus occupies a position very slightly posterior to the centre of the ventral surface.

The spiracles are situated on the outer portion of the supracoxal folds at the level of the fourth pair of coxae.

In addition to these larger openings the cuticle of *Argas persicus* is perforated by scattered pores. These pores, few in number, are found on both dorsal and ventral surfaces, and also on the appendages. They are very small and rudimentary. The hypodermal glands, so well developed in the *Ixodidae*, of which the cuticular pores are the external openings, are absent in *Argas persicus*.

The external sensory organs are apparently limited to the tactile hairs and *Haller's organ* (see Pl. II, fig. 4, *Hal.org.*, and Pl. VI, fig. 26). The tactile hairs, which are distributed over the surface of the body and appendages, are for the most part isolated, but in certain places, notably the terminal extremities of the palps, they are grouped together, in a dense cluster (see Pl. IV).

Haller's organ is a small vesicle containing sensory hairs situated on the tarsi of the first pair of legs. Its cavity communicates with the exterior by a minute pore. The olfactory function of Haller's organ is now definitely established[1]. *Argas persicus* is extremely sensitive to light but definite organs of vision can not be identified.

In general appearance, the adults of both sexes resemble each other very closely. The male is usually smaller than the female, but this rule is by no means invariable. The sexes are readily distinguished by the shape and size of the genital aperture (see Pl. III, figs. 3 and 4, *gen. ap.*). In the male, its transverse diameter is considerably narrower than the width of the basis capituli and the lips of the opening have an elliptical or half-moon shaped contour. The genital aperture of the female is a sharply defined transverse slit, the length of which is as great as, or exceeds, the width of the basis capituli.

The nymphs closely resemble the adults in general appearance. Their smaller size and the absence of a genital aperture are the more obvious points of distinction. The discs are not so numerous, especially in the neonymph.

The larvae are small hexapodous creatures, the 4th pair of legs not being developed; the spiracles are absent and the discs of the later stages are represented by a single circular area in the centre of the dorsum. The capitulum of the larva is situated so far forward as to nearly approach the almost terminal situation of this structure as seen in the *Ixodidae*. Until engorgement takes place, the greater part of the capitulum is visible from the dorsal aspect; after engorgement, the anterior margin of the body generally extends so far forward as to entirely conceal it. The capitulum of the nymph also occupies a position relatively more anterior than that of the adult, though never so far advanced as that of the larva. In the unfed *neonymph*[2], it is generally possible, from the dorsal aspect, to see the tip of the hypostome protruding beyond the anterior margin of the body.

[1] Hindle, E. and Merriman, G. (1912).

[2] = 1st stage nymph.

The Integument.

Plate III.

The integument is comprised of two layers—an inner layer of living cells, forming the *hypodermis,* and an external chitinous *cuticle,* a product of the activity of the hypodermal cells. The consideration of the structure of the hypodermis and its relations with the superimposed cuticle is reserved for a subsequent section of this paper; the present is only concerned with the cuticular structures.

To the naked eye, the cuticle of *Argas persicus* presents the appearance of a leathery investment with a finely granular surface, which is interspersed with small, slightly depressed, glistening areas of darker colour and rounded or elliptical outline.

If the cuticle is removed, in the manner described in a previous section (p. 23), a complete preparation of the cuticle of the dorsal and ventral surfaces may be obtained. From such a preparation it is seen that the granular appearance of the cuticle is due to the fact that almost the entire surface of the body is divided by a network of fine, undulating wrinkles into a mosaic of minute areas (see Pl. II, fig. 3). These cuticular areas are of three kinds, viz.:—*a,* the *discs*; *b,* the *scutellae*; and *c,* the *marginal scutellae.* The discs (*dc.*) are most conspicuous by reason of their greater size and darker colour. They are disposed in regular order over the entire dorsal surface of the body; on the ventral surface, however, they are limited to the marginal and post-anal portions. Towards the margins of the body, the discs are small and numerous, and, for the most part, are arranged in radially disposed series. On the median field of the dorsum they are usually larger and more isolated. The entire remaining surface of the body, with the exception of certain limited portions, is covered by small areas —the scutellae (*sc.*)—which form a mosaic-like filling between the discs. The scutellae are absent from the skin of the appendages, the greater portion of the coxal and supracoxal folds, the camerostome, with its folds, the post-genital area, the perianal area, and a small lozenge-shaped area situated in the median line towards the anterior end of the dorsum. On both dorsal and ventral surfaces, the margin of the body is outlined with a single row of more or less quadrangular areas—the marginal scutellae (*sc.m.*). These differ from the ordinary scutellae in their shape, their greater size, and in the fact that they are often compound As seen by transmitted light, the discs and both forms of scutellae each

appear to be surrounded by a broad margin which encloses a central rounded or polygonal area. In vertical section, all three forms are seen to be raised areas of the cuticle, deeply hollowed on the internal surface and slightly depressed on the outer surface, the central portion of each area thus being biconcave (see Pl. III, figs. 1 *a*, 2 *a*, and 2 *b*). The central area seen by transmitted light in flat preparations is the outline of the internal depression.

The scutellae are each furnished with a very short stout curved hair. Many of the marginal scutellae are compound, and bear two, three or four hairs, a corresponding thinning of the chitin underlying them. The discs resemble the scutellae in the appearance of their section, but never bear hairs. The internal surface of their central area is divided by a network of fine ridges (see Pl. III, figs. 1 and 2, *imp.m.*) into a large number of polygonal areas, these representing the impressions of the individual fibres which form the muscle-columns, the extremities of which, as already pointed out, find their cuticular attachment on the internal surface of the discs. As the disposition of the discs is determined by the anatomical arrangement of the body-muscles, the subject will be more conveniently dealt with in connection with the description of the musculature.

The interstices between the discs and scutellae are filled with softer and more pliable chitin, the surface of which is thrown into short, irregularly undulating ridges.

In the general structure of its details, the integument of the nymphal forms agrees with the foregoing description of that of the adult. In the neonymph, the discs are few in number, the scutellae are not so closely crowded, and in consequence the soft, wrinkled, interstitial integument is more extensively developed. The marginal scutellae, on the other hand, are as well-established as in the later stages.

In the larva, the structure of the integument is strikingly different from that of the nymphal and adult forms. It shows a closer approach to that of the larval integument of the *Ixodidae*. The scutellae are entirely absent, and the discs are represented by a single circular area on the middle of the dorsal surface. The cuticle of both dorsal and ventral surfaces is covered with fine, more or less parallel ridges which bear a slight resemblance to the pattern of a finger-tip impression. The surface of the body is scattered with relatively large hairs. The ridges of the integument are most pronounced in the posterior portion of the body, and to the fact that they are continuous from the dorsal to

the ventral surface, is due the crenulated appearance of the posterior margin of the body in mounted specimens. The hairs, particularly those situated on the posterior portions of the body, are often slightly serrated, and in many cases the truncated tip is split into two, three or even more fine points. The supracoxal and coxal folds are barely developed.

The Genital Orifice.

Plate I, fig. 2; Plate II, fig. 4; and Plate III, figs. 3, 4 and 7.

In both sexes the genital orifice is situated in the mid-ventral line, about the level of the first intercoxal space. Its position is subject to some slight degree of variation, particularly in the case of the female, in which it tends to move towards the basis capituli as the time of oviposition approaches.

As already stated, the size and appearance of the genital orifice afford a ready means of distinguishing the sexes.

The genital orifice of the female (see Pl. III, figs. 4 and 7, *gen.ap.*) is a conspicuous, transversely placed slit with more or less tumid lips. The posterior lip protrudes so far as to just overlap the anterior lip, the margin of which is thus concealed when the aperture is closed. The actual opening is, in consequence, directed forwards towards the capitulum, an arrangement which is obviously associated with the remarkable process of oviposition. The posterior lip of the genital aperture is continued backwards without interruption into the post-genital area, the outline of which is roughly that of an equilateral triangle with a posteriorly directed, truncated apex. The cuticle of both genital opening and post-genital area is sufficiently pliable and extensile to allow of a considerable amount of stretching during the passage of the relatively large ova.

The cuticle is reflected inwards at the margins of the genital orifice, and forms a continuous chitinous lining to the vagina, extending as far as the point of junction of the latter with the uterus. The reflected margin of both lips of the genital orifice is beset with short, stiff, curved hairs, which are particularly numerous on the anterior lip. The terminal portion of the vagina is capable of being completely prolapsed through the genital orifice, a condition which normally appears during the extrusion of the ova.

The genital orifice of the male (see Pl. III, fig. 3, *gen.ap.*) occupies a corresponding position, but is considerably smaller than that of the female. It has the form of a strongly arched, crescentic slit, the convexity

of which is directed towards the basis capituli. The extremities of the anterior lip are joined by a transverse fold of integument which completes an elliptical figure, and which covers the hinder portion of the posterior lip, in such a manner as to make it appear that the latter protrudes through a gaping opening from the interior of the genital canal. There is no trace of an intromittent organ; in coitus, the function of such an organ is performed by the capitulum.

The earliest trace of a genital orifice is seen towards the latter end of the second nymphal stage (*deuteronymph*), by which time a small dimple-like depression is found to occupy the site of the genital orifice of the adult.

The Anus.

Plate I, fig. 2; Plate II, fig. 4; and Plate III, fig. 5.

In all the stages, the anus is situated in the median line, near, but slightly posterior to, the centre of the ventral surface. It has the form of a short longitudinally disposed slit (see Pl. III, fig. 5, *an.ap.*), the margins of which are supported by a pair of stout *anal valves* (*an.v.*). The whole structure is surrounded by a slightly raised *annulus* (*an.m.*) of thickened cuticle, which gives it a more or less elliptical contour, the major axis of which is longitudinal. In the immature stages, the contour of this anal annulus approaches a more circular form, and the transverse diameter occasionally may slightly exceed the longitudinal. The anal valves, which have a semilunar form, are merely thickened portions of the cuticle, to the internal surface of which the anal muscles are attached. Towards their straight, mesial margins, they bear an irregular row of hairs, variable in number, which overhangs and guards the anal slit. In the larva, only a single pair of these anal hairs is developed. The cuticle is continued through the anal opening and forms a continuous, but very thin, chitinous lining to the anal canal. The actual lips of the anal slit are formed by the slightly prolapsed folds of this delicate cuticle which are seen between the anal valves. The valves are freely articulated to the anal annulus by the intervening thin soft cuticle.

The Spiracles.

Plate II, fig. 4, *sp.*; and Plate III, fig. 6.

The spiracles are situated on the outer slope of the supracoxal folds, on a level with the bases of the coxae of the fourth pair of legs. Compared with the spiracles of the *Ixodid* ticks, they are small and

inconspicuous, and the fact that they are more or less concealed by the third pair of legs, makes their recognition in the living animal a little difficult.

In the published descriptions, the spiracles of *Argas persicus* have been stated to have a crescentic or semilunar form. If, however, their structure is compared with that of the spiracles of the *Ixodidae*, it at once becomes apparent that the above description applies with accuracy to a portion of the spiracle only. As a matter of fact, the actual form is ovoid, or more or less circular. Each spiracle appears externally as a slightly elevated, convex boss, the surface of which is divided by a deep, narrow and curving cleft into two, structurally different portions. The anterior portion (see Pl. III, fig. 6, *a.por.*) has a crescentic form, and is perforated by innumerable minute pores which are distributed over its entire surface. The posterior portion (*mac.*) is formed of ordinary cuticle which is continuous with the general integument. Between these two areas the cleft (*os.*) leads down and opens into a large *atrial cavity* which lies beneath the spiracle, and from which the tracheae take their origin. The anterior portion corresponds, therefore, to the *area porosa* of the spiracle of the *Ixodidae*. The cleft is the *ostium* of the spiracle, and from its relations the posterior imperforate portion can not be other than the homologue of the *macula*. As will be shown in a subsequent section of this paper, the internal anatomy of the spiracle fully bears out the above comparison.

The obvious point of difference in structure between the spiracles of *Argas persicus* (this applies, so far as we know, of the spiracles of the *Argasidae* collectively) and those of the *Ixodidae* is that, in the former, the extent of the porose portion of the spiracle is limited to the anterior and lateral margins of the macula, while in the more highly specialised *Ixodidae* the porose portion has developed so as to completely surround the macula and to isolate it from the general integument.

Apart from the matter of size, the spiracle in the nymphal stages is similar in all respects to that of the adult.

The Coxal Glands.

In both adult and nymphal stages a single pair of coxal glands is present, the ducts of which open, one on either side of the body, immediately behind the posterior margin of the coxae of the first pair of legs (see Pl. III, fig. 7, *o.cx.gl.*). The opening is elongate and slit-like and follows the contour of the coxa. It is generally concealed by a prominent fold of the integument, which projects in the interspace between

coxae I and II; in dried specimens, however, it frequently happens, owing to the shrinking of the cuticle, that the fold is obliterated and the gaping aperture is then quite apparent.

The actual site of the opening is often demonstrated in a curious way. When living specimens are immersed in Carnoy's fluid for fixation, the operation causes the ticks to expel a quantity of the secretion of the coxal glands which coagulates in the form of an adherent flocculent tuft, immediately on coming into contact with the reagent.

We have not identified the coxal glands in the larva.

Gené's Organ.

A detailed description of the structure and relations of this remarkable organ, which is only found in the female, is reserved for a later section: the present is only concerned with those parts which are visible on external examination.

The external opening of Gené's organ is situated in the lower part of the camerostomal depression, immediately anterior to the fold formed by the fusion of the dorsal surface of the basis capituli with the roof of the camerostome (see Pl. III, fig. 7, *o.Gen.org.*). It occupies the entire width of the camerostome and, on account of its somewhat prominent and slightly everted lips, is readily seen when the capitulum is sufficiently depressed to expose the lower part of the camerostome.

The Capitulum.

Plate IV, figs. 8, 9, and 10; Plate V, figs. *A–K*;
Text-fig. 2.

In common with all the *Ixodoidea*, the first and second pairs of appendages of *Argas persicus*, in conjunction with the buccal cavity and pharynx, have undergone an extreme degree of modification, forming a complex and remarkable structure which articulates with the anterior portion of the prosoma. The complete arrangement is termed the capitulum.

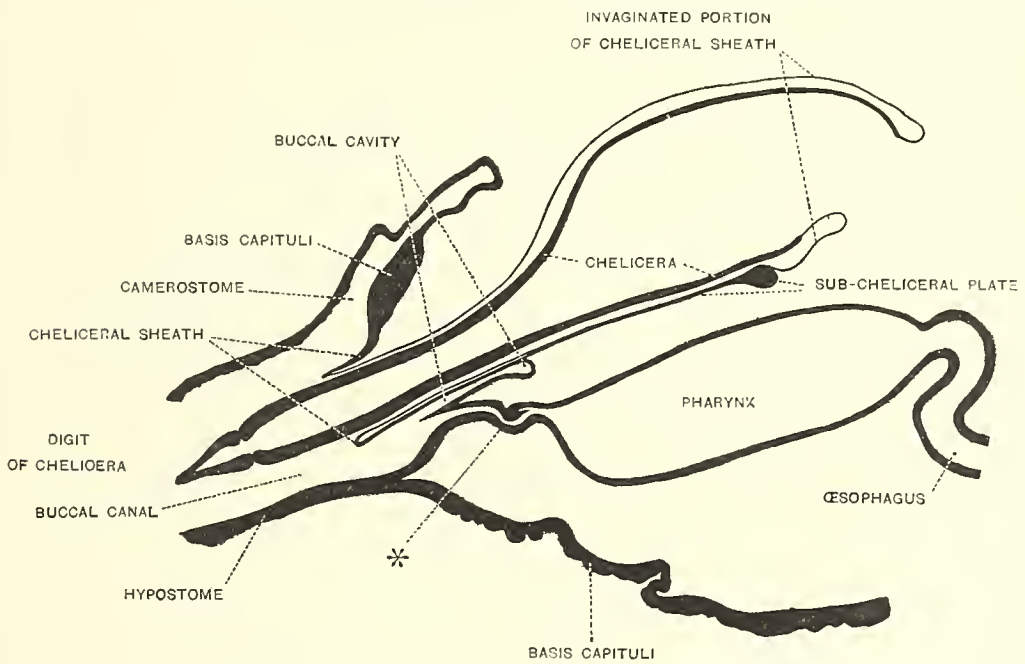
In spite of the alteration, due to this specialization, a homological comparison, of the various parts of which the capitulum is composed, with the corresponding parts of the typical *Arachnida*, is not a matter of great difficulty[1].

[1] See Jourdain, S. (1901), and Bonnet, A. (1907).

The position and general relations of the capitulum have already been alluded to (p. 26). The ventral situation of the organ, as seen in the *Argasidae*, in contradistinction to the terminal situation exhibited in the *Ixodidae*, is due, in all probability, not so much to a shifting backwards of the capitulum, as to a forward extension of the body. It has been shown that in the larval stage the capitulum is almost terminal, and that the apparent backward movement is progressive through the nymphal stages.

The Basis Capituli.

The basis capituli (*b.c.*) comprises the whole proximal portion of the capitulum. Seen *in situ*, from the ventral aspect (see Pl. IV, fig. 8), the outline is roughly rectangular ; the lateral margins are slightly



Text-fig. 2.

The asterisk indicates the constricted pharyngeal orifice.

convex and the structure becomes narrower anteriorly. The postero-ventral margin is concealed by a transverse fold of the ventral integument. From the lateral aspect (see Text-fig. 2) the basis capituli is seen to taper down in its distal portion, and thus presents a somewhat conical outline. The entire base is open and communicates with the body cavity through a large foramen in the ventral body wall. The posterior rim of the basis is attached all round to the margins of

this foramen by a thin articular cuticle which forms a deep invaginated fold along the dorsal margin, to allow free movement in the act of depression of the capitulum. The basis capituli is freely articulated with the prosoma and is capable of a considerable degree of movement in the sagittal plane.

The walls of the basis capituli are formed of stout and resistant chitin which affords a firm attachment for certain muscles. The ventral wall of the basis capituli is prolonged anteriorly, in its median portion, to form the hypostome (*h.*), on either side of which the basal articles of the palps (*p.i.*) are inserted. On the dorsal side, the basis capituli narrows down to form what is at first a sheath common to both chelicerae; this bifurcates almost immediately and is prolonged forwards to form a pair of tubular sheaths (*s.ch.*), through which the chelicerae protrude, the whole arrangement resembling a short pair of trousers. The opening of the mouth lies concealed between the basal portions of the hypostome and the chelicerae, and is hidden from lateral view by the bases of the palps. On the ventral surface of the basis capituli, a number of hairs are borne. Of these, four are conspicuous, viz. a pair of *post-hypostomal hairs* (Pl. IV, fig. 8, *p.h.h*) situated near the median line, immediately behind the base of the hypostome, and a pair of *post-palpal hairs* (*p.p.h.*) which are situated a short distance behind the bases of the palps. A few stumpy hairs occupy the lateral portions of the ventral surface. The dorsal surface is scattered with numerous, anteriorly directed hairs, which, together with those on the palps and the roof of the camerostome, serve to exclude foreign matter from the camerostomal depression (see Pl. III, fig. 7).

The Chelicerae.

Plate IV, figs. 8, 9 and 10; Plate VI, figs. 22–25.

The chelicerae, which form the first pair of appendages, are situated above the oral opening and buccal cavity. Their free, distal extremities protrude anteriorly for a considerable distance in front of the actual opening of the mouth and their posterior ends extend backwards, through the basis capituli and the capitular foramen, into the body cavity. Each consists of a stout, more or less cylindrical shaft (*sh.ch.*), the proximal half of which is dilated (*b.ch.*). The distal extremity of the shaft bears a terminal, modified chelate digit (*d.ch.*).

The chelicerae slide freely, backwards and forwards, within the sheaths (*s.ch.*) formed by the basis capituli. Their shafts are connected

with the sheaths by a thin membranous invagination of the latter. This inner sheath (*s.ch'.*) is formed by the inflected distal margin of the outer cheliceral sheath which is invaginated between the outer sheath and the shaft, and passes backwards as far as the base of the latter, where it is again reflected forwards and continues directly into the margin of the expanded base of the cheliceral shaft. The relations of these parts are clearly shown in the longitudinal section of the capitulum (Text-fig. 2) and in the transverse sections of the capitulum (Pl. V, figs. 11–20). Posterior to the buccal cavity, the ventral portion of the inner membranous sheath is fused, to a limited extent, with an internal chitinous structure, the *sub-cheliceral plate* (see Pl. V, figs. 19 and 20, *sub.ch.p.*, also Text-fig. 2), but becomes free again in its posterior portion, where it forms the loose reflected fold which continues directly into the posterior extremity of the cheliceral shaft, thus allowing the necessary freedom of movement for the protrusion of the chelicerae.

Rotation of the chelicerae within their sheaths is prevented by the fact that the mesial face of the expanded basal portion of each is flattened, and the two plane surfaces are permanently maintained in close apposition (see Pl. V, figs. 19 and 20). Unlike the *Ixodidae*, the dorsal surfaces of the cheliceral sheaths are not "shagreened." The separation of the two sheaths commences on the ventral surface of the common sheath (see p. 36) as a median fold of chitin, which commences posteriorly at the level of the opening in the floor of the buccal cavity leading to the pharynx (see Pl. V, fig. 15). As it runs forwards, this median fold dips more and more deeply between the two cheliceral shafts (see figs. 14 and 13) and finally fuses with the dorsal wall of the basis capituli (fig. 13) which divides at this point (fig. 12) and thus completes the separate sheaths (figs. 12 and 11). Owing to the fact that the cheliceral sheath extends further forwards on the dorsal side of the chelicera, only this portion figures in the first section (fig. 11) of the series represented on Plate V, which passes through the extreme portion of the sheath.

The chelicerae are retracted by a pair of stout muscles which are inserted into the posterior extremities of the shafts. These retractor muscles pass directly backwards and upwards, and are attached to the under surface of the dorsal cuticle, where their insertions are indicated externally by the two large obliquely placed oval discs situated on either side of the median line of the dorsum at the posterior limit of the anterior fourth of the body length (see Pl. II, fig. 3). Protrusion

of the chelicerae is effected, not by direct muscular action, but by a general contraction of the dorso-ventral body-muscles. By the pressure thus created within the body cavity, the chelicerae are thrust out through their sheaths until further movement is stopped by the expanded basal portions coming into contact with that portion of the basis capituli which forms a common sheath (see Text-fig. 2) round the two cheliceral shafts.

The cavity of the expanded proximal portion of the cheliceral shaft is completely filled by the *flexor* and *extensor muscles* which operate the *digit*. The tendons of these muscles pass forwards through the narrow distal portion of the shaft to their terminations at their respective places of insertion into the digit, each being furnished with a guide, in the form of a narrow chitinous canal which runs in the thickened wall of the shaft. The guiding canal of the *flexor tendon* (Pl. VI, figs. 22–24, *t.f.d.*) is situated in the lateral portion of the wall of the shaft and extends from the commencement of the contracted portion of the latter, almost to the articulation of the digit. This is clearly shown in the transverse sections of the capitulum (see Pl. V, figs. 11–15). The *extensor tendon* (*t.e.d.*), which is the more slender of the two, is situated towards the internal and dorsal portion of the shaft. Its guiding canal is neither so well-developed nor so extensive as that of the flexor tendon and is not shown in the sections on Pl. V.

The *digit* of the chelicera (Pl. IV, figs. 8, 9 and 10, *d.ch.*; Pl. VI, figs. 22–25), which forms the terminal portion of the appendage, has received considerable attention in the past, chiefly as a result of the idea that the forms of its component parts are of value for the purpose of specific determination. The structure is, however, subject to no inconsiderable amount of individual variation, and, moreover, its preparation for such an examination involves not only its removal from the specimen, but, on account of its minute size, a troublesome process of mounting. For both reasons therefore an account of the digit is best omitted from specific descriptions.

In the fact that it is comprised of two mobile articles, the digit of the chelicera conforms to the chelate type generally found in the *Arachnida*; but, in accordance with the mode of life followed by the tick, the usual pincer-like organ has been modified to form a cutting-organ, pure and simple.

The larger *internal article* (*i.a.*) has the form of an irregular triangular pyramid, the apex of which terminates in a laterally directed cusp. It is attached by its expanded base to the extremity of the

cheliceral shaft, which forms a broad articulatory surface on which the entire digit rocks. On the dorso-lateral surface, a chitinous outgrowth, the *dorsal process* (*d. p.*), appears. This is a crescentic structure, the two pointed cusps of which protrude in a lateral direction. The ventro-lateral face of the internal article is excavated about the middle of its length in the form of a deep fossa into which the base of the *external article* (*e. a.*) is articulated. The external article as seen in profile (*i.e.* from the dorsal or ventral aspect) presents a triangular outline, the side of the triangle being produced laterally in a series of curved, reflexed cusps, usually three in number, which increase in size from before backwards. The form of these cusps, as well as their number, is apt to vary in individual specimens, but those illustrated (Pl. VI, figs. 22 and 24) show the most frequently occurring types.

Both articles of the digit, and also the dorsal process, are hollow, and their internal cavities communicate with each other, and that of the internal article is directly continuous with the internal cavity of the cheliceral shaft. The cavity of the internal article also communicates with the exterior by means of a large pore (*pr.*), which penetrates the lateral wall of the expanded base a little distance below the insertion of the external article. The flexor tendon of the digit divides at the base of the internal article into two branches, the larger of which is inserted into the base of the internal article and the smaller passes upwards to be inserted into the base of the external article. These and the extensor tendons of the digit are represented in the sections (Pl. VI, fig. 25, *e.* and *f.*), where they are distinguished by horizontal line shading.

The entire digit, with the exception of the pointed cusps and cutting-edges of the articles and dorsal process, is surrounded and protected by a delicate ensheathing structure which is conveniently termed the hood (*hd.*). The structure and relations of this hood, which appear to be less simple than is the case in the *Ixodid* ticks, are impossible to define from the examination of cleared specimens alone, on account of the extreme transparency of the parts. For this purpose, recourse must be made to serial sections passing through the entire structure. It is then seen that the hood is entirely composed of soft membranous chitin and is partially derived from the cheliceral shaft, and partly from the digit itself. From its relations, it appears reasonable to suppose the hood represents an exuberant growth of the soft articulatory chitin of the joint between shaft and digit. On the internal side, the hood continues the outline of the cheliceral shaft forwards, and extends almost to the extremity of the internal article. The distal

margin slopes obliquely backwards, so that in its lateral portion it barely surrounds the base of the external article. With the exception of a limited free margin, the hood is always in intimate contact and more or less fused with the surfaces of the digit. Its relations with the articles are clearly shown in the transverse sections through the digit (Pl. VI, fig. 25, *a.–f.*). In these figures, the hood is distinguished by the darker, stippled shading, the articles of the digit being indicated by finer stippling on a clear ground. The free margin of the hood is slightly sinuous, and its extreme portion near the tip of the internal article is markedly serrated, the serrations presumably facilitating the retraction of the hood during the operation of biting.

In both sexes, and also in the immature stages, the foregoing description applies. Slight differences do actually exist, but are quite unimportant from the anatomical standpoint.

The Palps.

The second pair of appendages, termed *palps*, are borne on the antero-lateral angles of the basis capituli, one on either side of the medianally situated hypostome (see Pl. IV, figs. 8, 9 and 10, *p.*). Each consists of a more or less cylindrical appendage comprised of four, freely mobile articles, the lengths of which are approximately equal. In the state of rest, they are usually doubled up, in the manner shown in figs. 8 and 9 (Pl. IV).

The first or *basal article* (*p.i.*) is the largest in diameter and its length is about equal to its breadth. The proximal portion is partially telescoped into the large articulatory foramen in the wall of the basis capituli ; while the plane of the distal margin inclines downwards from the mesial side to the lateral face, thus giving the article, as seen from the ventral aspect, a rhomboidal outline. The free distal edge of the basal article surrounds the proximal part of the third article like a collar. An interesting feature, to be referred to again, is the development of two, pronounced, salient, longitudinal ridges which delimit the mesial face of the article dorsally and ventrally. Both ridges thin out to a fine edge, which overlaps the adjacent median structures—the basal portion of the hypostome ventrally, and the bases of the cheliceral sheaths posteriorly. In the ventral view of the female capitulum (Pl. IV, fig. 8), these ridges have been unfortunately omitted, but they are clearly shown in the transverse sections of the capitulum (see Pl. V, figs. 11–15). The mesial face of the article, the dorsal and ventral

margins of which are drawn out into these ridges, is flattened and often slightly concave. The *second* and *third articles* of the palp (*p. ii* and *p. iii*) call for no special remark. They are almost cylindrical, and like the basal article, are about as broad as long. The fourth and *terminal article* (*p. iv*) is appreciably smaller in diameter than the others. It tapers slightly, and terminates in a truncated, flattened, or even somewhat concave extremity, upon which is borne a dense cluster of short tactile hairs.

A comparison of the palp of *Argas persicus* with that of any of the *Ixodid* ticks, shows at once, that in the former more of the primitive characters of the Arachnid "pedipalp" are retained. In the *Ixodidae*, the palps have lost a good deal of their mobility, being freely articulated at the place of insertion into the basis capituli only, and the terminal article is reduced to a diminutive tactile papilla situated in a deep fossa on the ventral surface of the third article. The internal face of the palp, comprising the first, second and third articles, is always hollowed out in such a manner that in the state of adduction the palps partially ensheath the lateral surfaces of the median structures of the capitulum—the chelicerae and the hypostome. In *Argas persicus* the ridges of the basal article, described above, in all probability signify an approach to this condition, but the rudimentary attempt is limited to the single article.

A very few hairs appear on the ventral surfaces of the palp, but as previously mentioned the dorsal surfaces are scattered with numerous anteriorly directed hairs, which, in conjunction with corresponding hairs on the roof of the camerostome and the dorsal surface of the basis capituli, serve the purpose of excluding dirt from the camerostomal depression.

The Hypostome.

The *hypostome* (*h.*) is a median prolongation of the ventral portion of the basis capituli. Proximally it forms the floor of the buccal cavity, and its distal portion is apposed to the ventral surfaces of the chelicerae, the three structures collectively forming a piercing and sucking organ or proboscis. The base of the hypostome is wide, but the lateral margins rapidly converge and follow a nearly parallel course from the middle of the organ to its distal extremity. With the exception of the tip, which is flattened, the ventral surface is strongly convex from side to side, and its distal half is armed with stout, recurved denticles which are disposed in more or less regular longitudinal rows. The arrangement

of the denticles is not so uniform as is usually the case in the *Ixodid* ticks, and is subject to a considerable amount of variation. As a rule, the tip of the hypostome bears a number of small denticles arranged in two or more irregular transverse rows. These are followed by some sixteen large denticles, disposed in two files on either half of the hypostome, and these again are followed by a series of rows of smaller denticles which decrease in size from before backwards and vanish completely about the middle of the length of the hypostome. The denticles do not as a rule extend to the lateral margins. The ventral surface of the hypostome is divided down the centre by a longitudinal furrow which gradually becomes obliterated some little distance posterior to the denticles. The dorsal surface, on the other hand, is deeply concave from side to side, and towards the hinder part a deep longitudinal depression, the hypostomal gutter (*h.g.*), arises, which, after running for a short distance backwards along the surface, is continued directly into the pharyngeal opening.

The basal portion of the hypostome is hollow, its cavity being continuous with that of the basis capituli behind, and continued forwards as a pair of fine canals which run on either side of the median line and terminate blindly some little distance behind the extremity. Like the chelicerae, the slight differences, exhibited in the form of both palps and hypostome, in the two sexes and in the immature stages, have no morphological significance. The foregoing descriptions apply more particularly to the female.

The Buccal Cavity.

Plate V, figs. 16 and 18; Plate VI, fig. 21.

The intimate relationship which exists between the buccal cavity and the capitulum makes it desirable to proceed with its description in the present section rather than to postpone it to a subsequent section dealing with the alimentary canal.

An examination of the two sections (fig. 15 and fig. 16 (Plate V)), will show that where the base of the hypostome merges into the ventral wall of the basis capituli, its lateral margins fuse with the ventro-lateral walls of that part of the basis capituli which is continued forwards above the mouth to form the cheliceral sheaths. In section (fig. 15) the hypostomal margins are still free, but in the following section (fig. 16), union has occurred and the space thus enclosed is the buccal cavity.

The floor of the buccal cavity is prolonged anteriorly in the form of a tongue-like process (*tg.*), which covers in the pharyngeal orifice. Apparently the function of this tongue-like process is to close the pharyngeal opening (*o.ph.*) while the salivary secretion is being forced directly into the wound made by the proboscis of the tick. The buccal cavity terminates in a cul-de-sac some little distance behind the pharyngeal orifice, into the postero-lateral angles of which the salivary ducts (*d. sal.*) open.

The chitinous structures in this part of the capitulum are very complicated, as a study of the series of sections on Plate V will show. The basal portion of the hypostome where it forms the floor of the buccal cavity and where it abuts on the foramina in the basis capituli, into which the basal articles of the palps are inserted, is much thickened, thus giving a high degree of rigidity to the basis capituli. The *sub-cheliceral plate* (*sub.ch.p.*) is a backward extension of the roof of the buccal cavity to which the dorsal dilator muscles of the pharynx are attached and which, as already mentioned, forms a guide upon which the expanded basal portions of the cheliceral shafts slide. Further reference will be made to these internal structures of the basis capituli in connection with the description of the alimentary canal.

The Legs.

In common with all the *Ixodoidea*, both nymphal and adult stages possess four pairs of well-developed ambulatory appendages; but, as has been remarked previously, the fourth or hindermost pair is suppressed in the larval stage.

The legs are of moderate length, though relatively shorter than is the case in the majority of the *Ixodidae*. They are borne on the anterior half of the ventral surface of the body, the two anterior pairs being directed forwards and the two posterior pairs backwards (see Pl. I, figs. 1 and 2, *l. i*, *ii*, *iii* and *iv*). Their colour is a pale yellowish-grey, and in the living animal they present a peculiar translucent glistening appearance. Each leg is typically six-jointed. The descriptive terminology of Arthropod appendages, which is in general use, may be conveniently applied in the present instance. Thus, the proximal or first article is termed the *coxa*; article 2, the *trochanter*; article 3, the *femur*; article 4, the *tibia*; article 5, the *protarsus*; and article 6, the *tarsus*. Each leg is terminated by a rudimentary *pulvillium*, upon which is borne a pair of curved claws. The proximal fifth of each of

the femora is divided from the remainder of the article by a joint-like constriction, constituting a pseudo-article (the *trochanterin* of Lahille).

The *coxae* (see Pl. I, fig. 2, *cx. i, ii, iii* and *iv*) have a more or less triangular contour, with rounded angles, and are set into apertures of corresponding outline which penetrate the ventral body wall. The fold of chitin which forms the actual joint between the coxa and the body wall extends, in part, for some little distance into the body cavity, and serves as a means of attachment for the coxal muscles. As previously stated, the coxae are not absolutely immobile. They are capable of a limited amount of adduction and abduction, a condition which is facilitated by the presence of the coxal and supracoxal folds. The *trochanter* (*tch.*) is the shortest article of the leg. Its form is roughly cylindrical and the length barely exceeds the breadth. The articulation of the trochanter with the coxa is such as to limit its movement to a plane which is more or less parallel to the ventral surface of the body. The three following articles, the *femur* (*fm.*), *tibia* (*tb.*) and *protarsus* (*pts.*), are of approximately equal length, that of the femur being slightly increased by the presence of the pseudo-article at its proximal end. Each of these articles is smallest at the proximal end the diameter increasing gradually to a maximum at the distal extremity. The greatest freedom of movement is found at the articulation of the femur with the trochanter which forms a universal joint; the remaining articulations only allow of movement in a single plane. The *tarsi* (*ts.*) are about equal in length to the three preceding articles, but instead of expanding distally, they become suddenly attenuated near the free extremity, the place of attenuation being marked, particularly in the case of the first two pairs of legs, by a pronounced hump. The tarsi of the first pair of legs are distinguished by the presence of Haller's organ (*Hal. org.*). The pulvillia are articulated with the reduced extremities of the tarsi. All the articles of the legs, with the exception of the coxae and trochanters, are slightly flattened in a dorso-ventral direction, and with the same exception they bear a small number of fine, short hairs which are arranged in scanty, longitudinal rows. The pulvillia (see Pl. VI, fig. 26) of the adult and nymph consist of a small segment or caruncle (*car.*) of irregular form, upon the slightly expanded extremity of which the claws are articulated. The collapsible pad, which is so conspicuous a feature of the pulvillia of the *Ixodidae*, is only represented by a slight puckering of the parts surrounding the bases of the claws (*pv.* in fig. 26). In the larva, on the other hand, the pulvillium is well developed (see fig. 27), and all the parts which exist in that of the *Ixodidae* can be recognised.

A minute segment, the caruncle (*car.*), forms a connecting link between the tarsus and the pulvillium proper. A curious feature is the presence of a roughened patch on the internal surface of each of the claws. This is not found in the nymphal or adult stages, and is doubtless associated with the different habit of life which is exhibited by the larva.

EXPLANATION OF PLATES I TO VI.

PLATE I. *Argas persicus.*

Fig. 1. Female; dorsal surface, ×8 diameters.
Fig. 2. Female; ventral surface, ×8 diam.

PLATE II. *Argas persicus.*

Fig. 3. Female; entire cuticle of dorsal surface, ×14 diam.
Fig. 4. Female; entire cuticle of ventral surface and appendages, ×14 diam.

PLATE III. *Argas persicus.*

Fig. 1. Female; portion of dorsal cuticle showing scutellae and two discs, ×170 diam.
Fig. 1*a*. Female; scutella in transverse section, ×170 diam.
Fig. 2. Female; portion of dorsal cuticle showing marginal scutellae, discs etc., ×170 diam.
Fig. 2*a*. Female; two adjacent discs in transverse section, ×170 diam.
Fig. 2*b*. Female; marginal scutella in transverse section, ×170 diam.
Fig. 3. Male; portion of venter, showing genital aperture, coxae etc., ×16 diam.
Fig. 4. Female; portion of venter, showing genital aperture, coxae etc., ×16 diam.
Fig. 5. Female; anus, ×170 diam.
Fig. 6. Female; left spiracle (opaque preparation), ×170 diam.
Fig. 7. Female; portion of venter, with capitulum depressed to expose opening of Gené's organ, ×30 diam.

PLATE IV. *Argas persicus.*

Fig. 8. Female; capitulum, ventral, ×150 diam.
Fig. 9. Larva; capitulum, ventral, ×190 diam.
Fig. 10. Larva; capitulum, dorsal, ×190 diam.

PLATE V. *Argas persicus.*

Figs. 11–20 (*A–K*). Male; transverse sections through the capitulum, showing the relations of the external and internal chitinous structures. The levels at which the individual sections pass through the capitulum are indicated by the letters *A–K* (see Pl. IV, fig. 8, and Pl. VI, fig. 21), ×110.

PLATE VI. *Argas persicus.*

Fig. 21. Female; buccal cavity, in optical section, to show relations between hypostomal gutter, pharynx, salivary ducts, etc., ×200.
Fig. 22. Male; chelicera, right, ventral aspect, ×350.
Fig. 23. Male; chelicera, right, lateral aspect, ×350.
Fig. 24. Female; chelicera, right, ventral aspect, ×350.

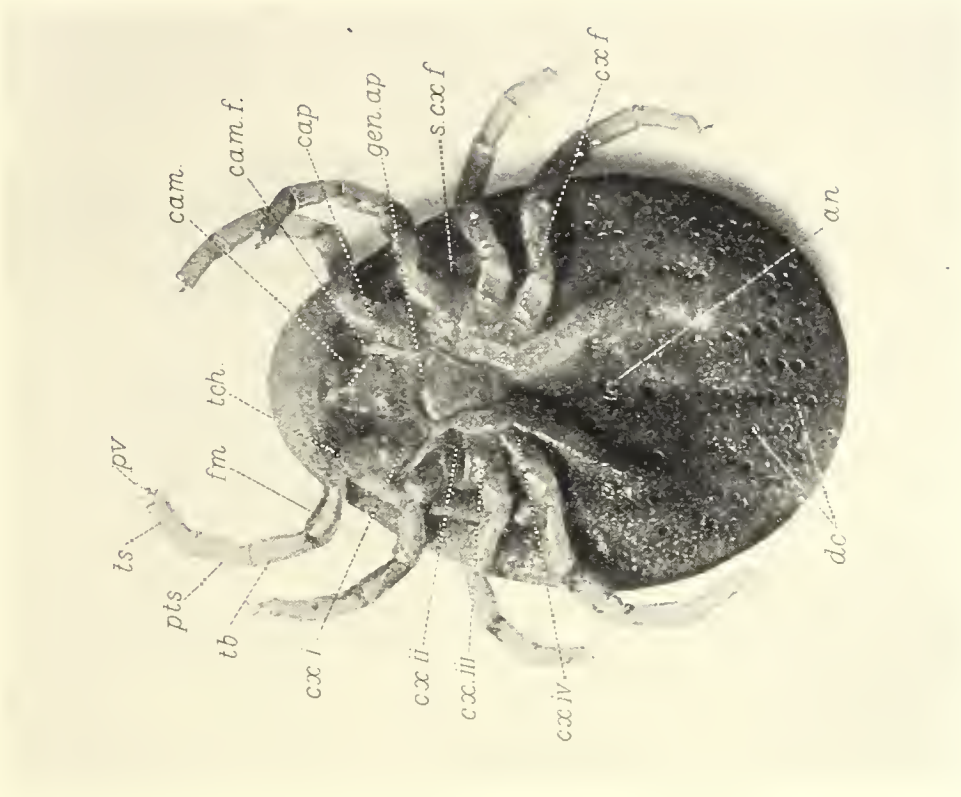
Fig. 25. Male; serial transverse sections through digit of left chelicera: *a.* at level of extremity of internal article and free margin of hood; *b.* at level of upper portion of dorsal process; *c.* at level of place of fusion of dorsal process with internal article; *d.* at level immediately below dorsal process; *e.* at level of lower portion of external article, showing divisions of flexor tendon of digit; *f.* at level of pore in base of internal article, showing extensor tendon and articulatory ligament of digit, ×500 diam.

Fig. 26. Female; tarsus rudimentary and pulvillium of leg I, showing Haller's organ etc., ×125.

Fig. 27. Larva; terminal portion of tarsus and pulvillium, ×125.

INDEX TO LETTERING ON PLATES I TO VI.

A, B, C, D, E, F, G, H, I and *K*	Indicating levels of transverse sections of the capitulum on Pl. V (see Pl. IV, fig. 8 and Pl. VI, fig. 21).
a.m.b.	anterior margin of body.
an.	anus.
an.ap.	anal aperture.
an.m.	anal annulus.
an.v.	anal valve.
a.por.	area porosa of spiracle.
b.c.	basis capituli.
b.ch.	expanded base of chelicera.
buc.can.	buccal canal.
buc.cav.	buccal cavity.
cam.	camerostome.
cam.f.	camerostomal fold.
cap.	capitulum.
car.	caruncle.
cc.al.	alimentary coeca.
ch.	chelicera.
cl.	claws.
cl'.	roughened area on claws of larva
cx.i, cx.ii, cx.iii, cx.iv.	coxae i to iv.
cx.f.	coxal fold.
dc.	disc.
d.ch.	digit of chelicera.
d.p.	dorsal process.
d.sal.	salivary duct.
e.a.	external article.
fm.	femur.
gen.ap.	genital aperture.
h.	hypostome.
Hal.org.	Haller's organ.
hd.	hood.
h.g.	hypostomal gutter.
h.m.	hypostomal margin.


cam.
cam.f.
cap
gen.ap
s.cx f
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cx ii
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cx iv
dc

Fig. 2.


l. ii
l. iii
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Fig. 1.

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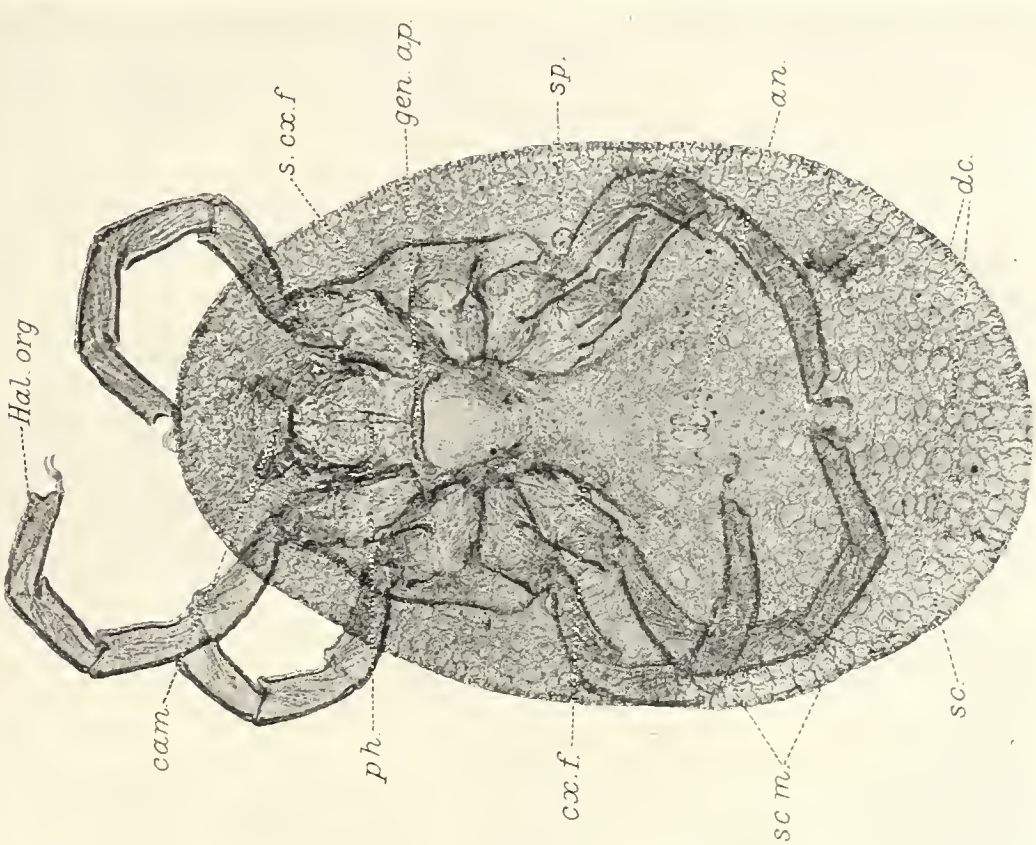

Fig. 4.

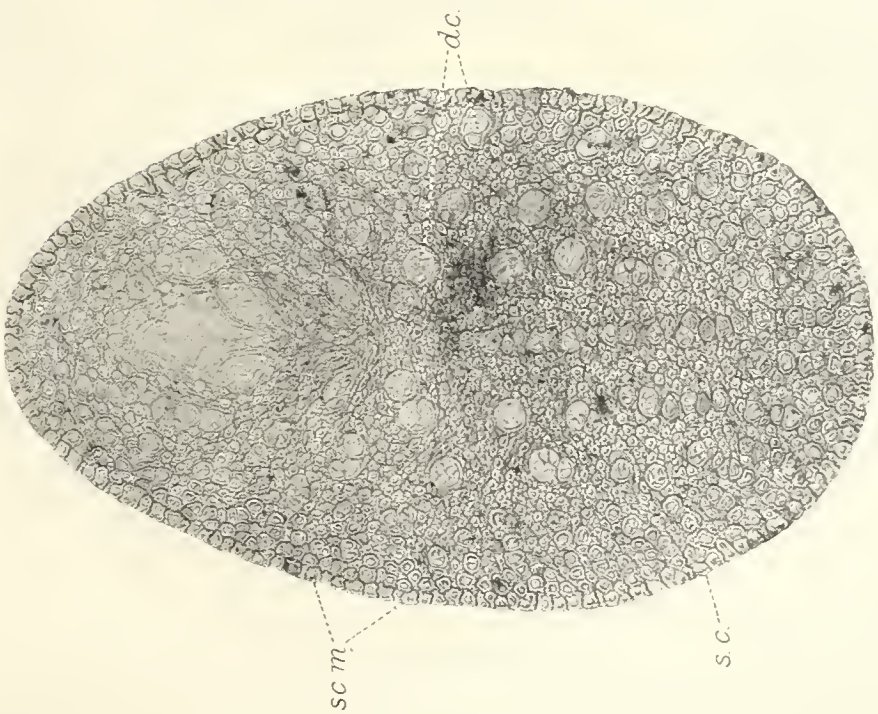

Fig. 3.

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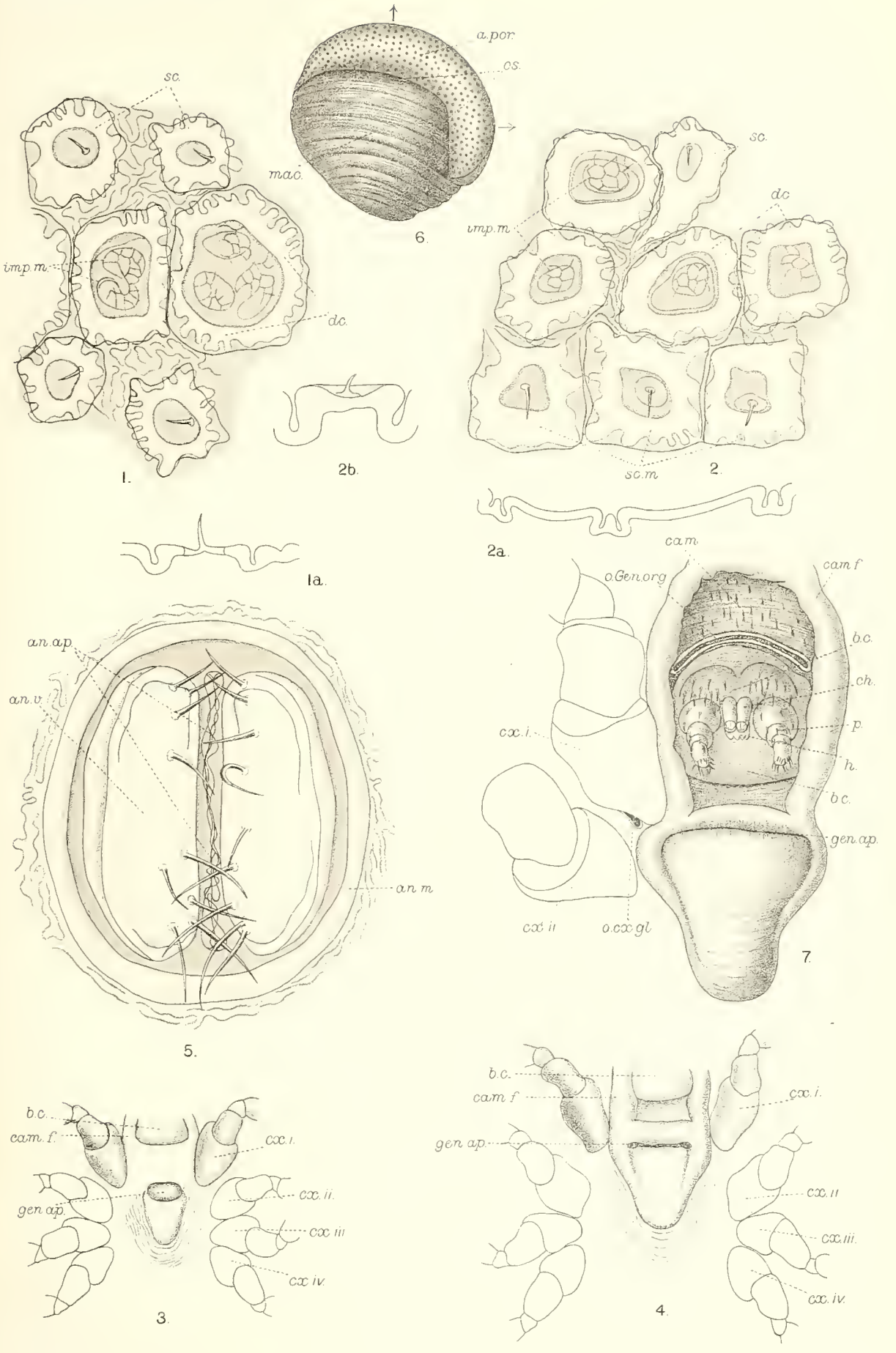

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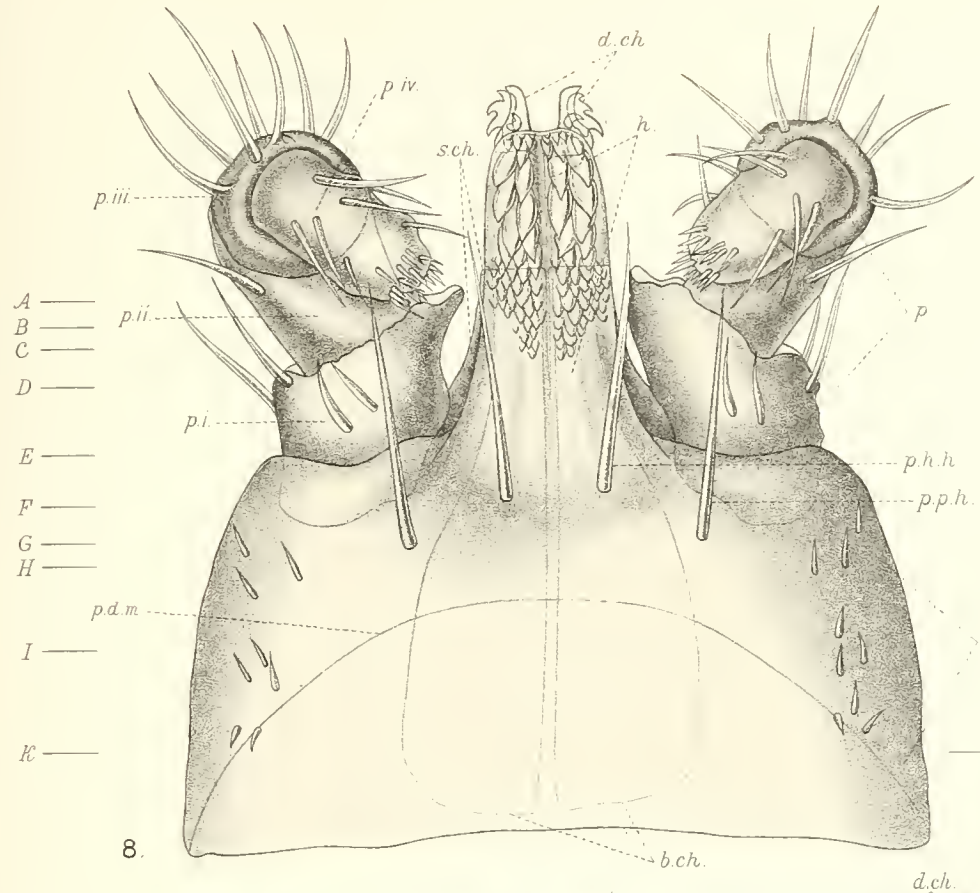

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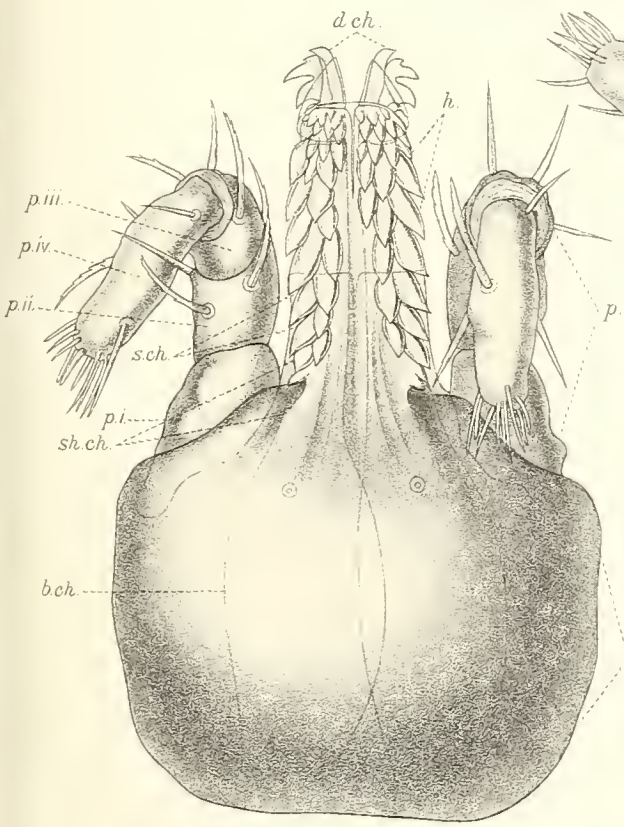

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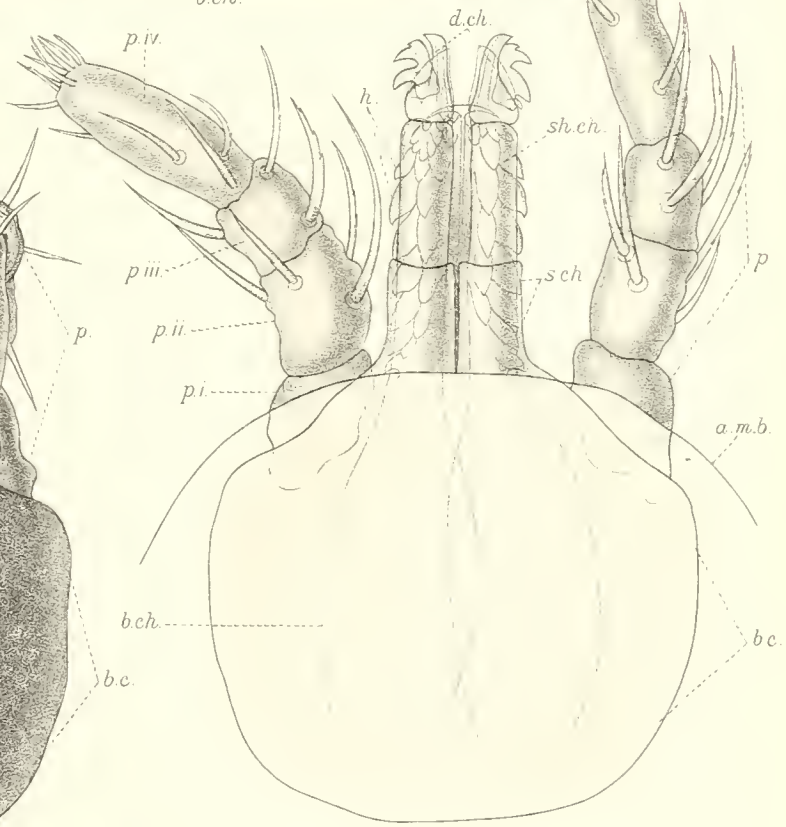

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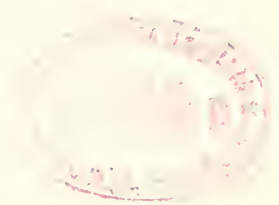
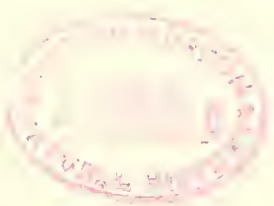
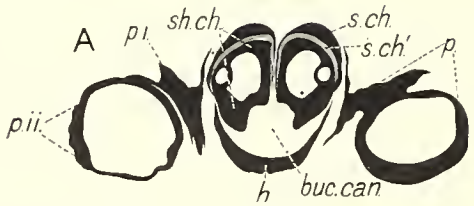
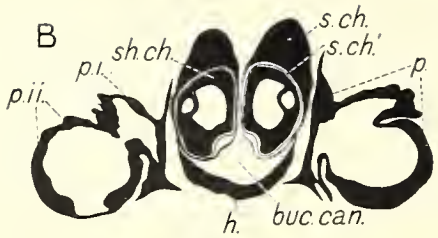






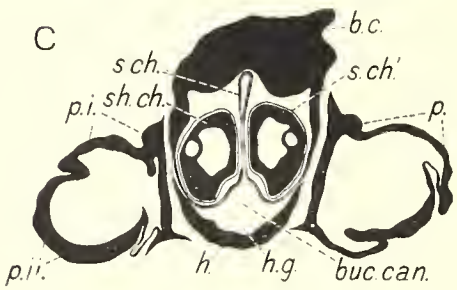
A. Fig. 11.



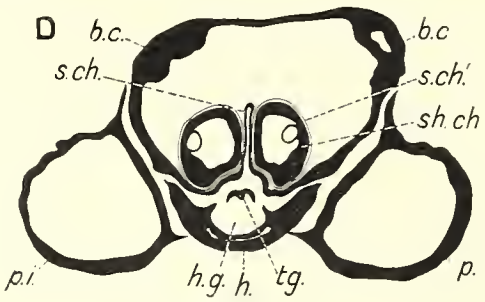
B. Fig. 12.

A. Fig 11. *A. persicus* ♂. Transverse section of capitulum passing through lower portion of Article 2 of the palps.

B. Fig. 12. *A. persicus* ♂. Transverse section of capitulum slightly lower than Section 1. Showing completion of cheliceral sheath.



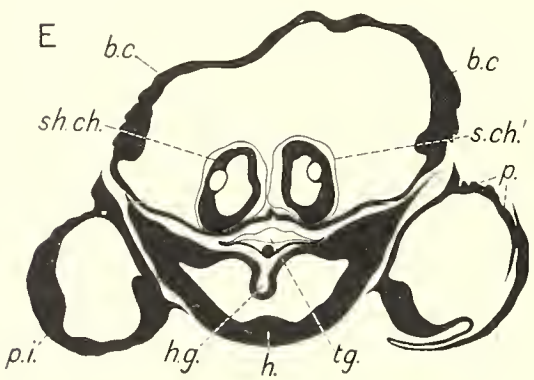
C. Fig. 13.



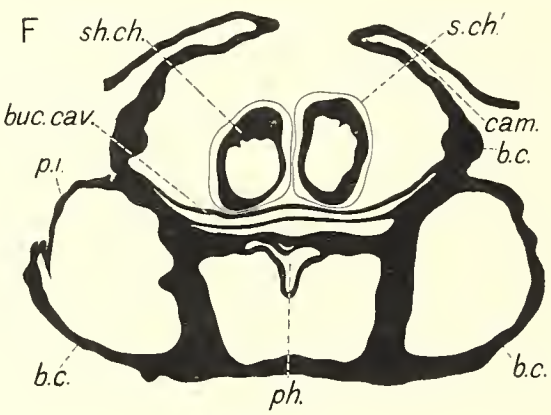
D. Fig. 14.

C. Fig. 13. *A. persicus* ♂. Transverse section of capitulum at level of junction of the bases of the two cheliceral sheaths.

D. Fig. 14. *A. persicus* ♂. Transverse section of capitulum through basal article of palps. Shows gutter on dorsal surface of hypostome leading posteriorly to the pharynx, also tip of tongue-like prolongation of the posterior part of the floor of the buccal cavity, which extends forwards over the pharyngeal aperture.



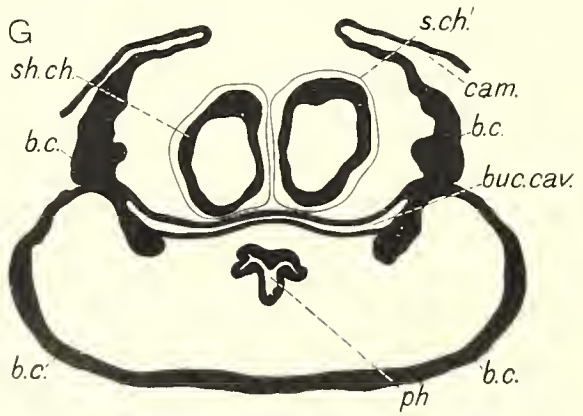
E. Fig. 15.



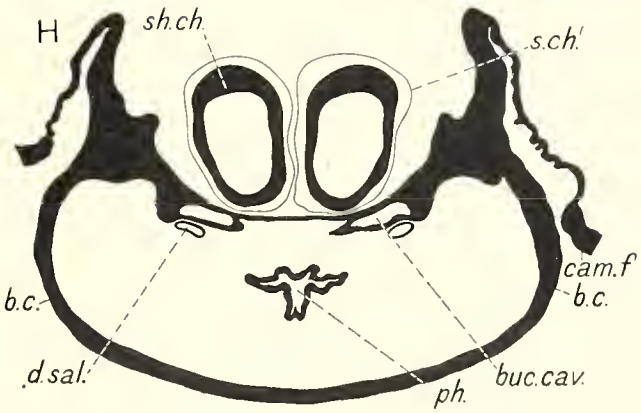
F. Fig. 16.

E. Fig. 15. *A. persicus* ♂. Transverse section of capitulum passing through basal portion of Article 1 of the palps.

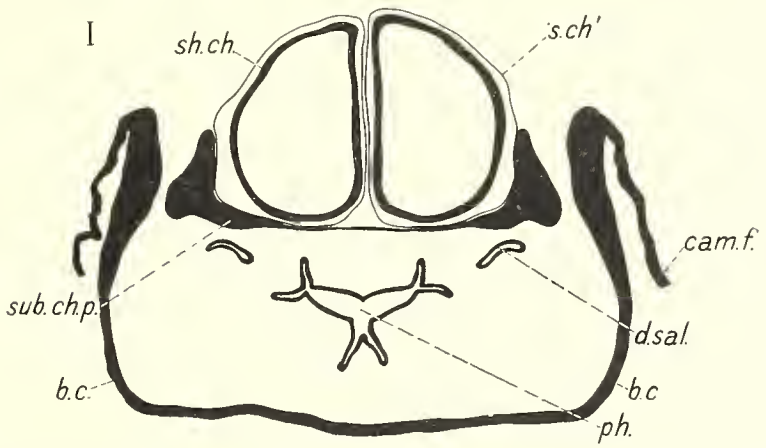
F. Fig. 16. *A. persicus* ♂. Transverse section through capitulum at level of commencement of pharynx.



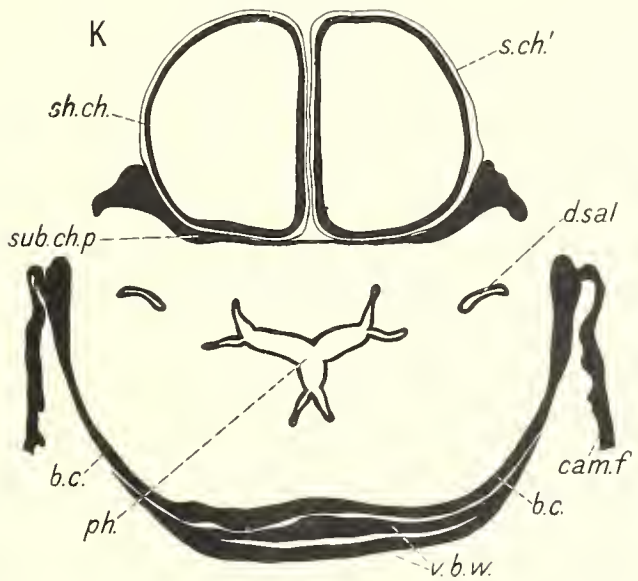
G. Fig. 17. *A. persicus* ♂. Transverse section of capitulum through upper portion of basis capituli.



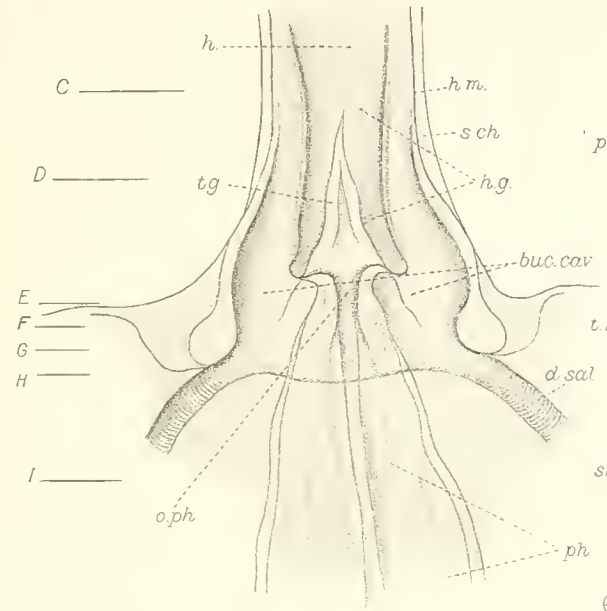
H. Fig. 18. *A. persicus* ♂. Transverse section of capitulum through posterior limit of buccal cavity, showing termination of salivary ducts.



I. Fig. 19. *A. persicus* ♂. Transverse section of capitulum through middle of basis capituli—showing relations of subcheliceral plate, salivary ducts, chelicerae and pharynx.



K. Fig. 20. *A. persicus* ♂ 10. Transverse section through capitulum at level of posterior limit of basis capituli.



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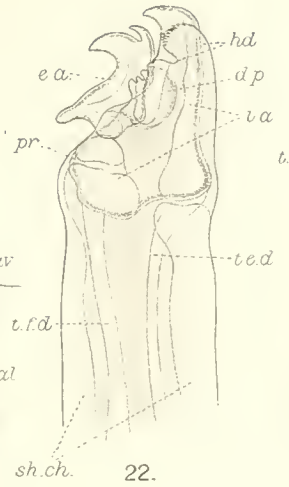

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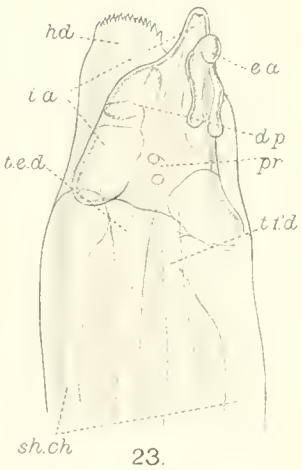

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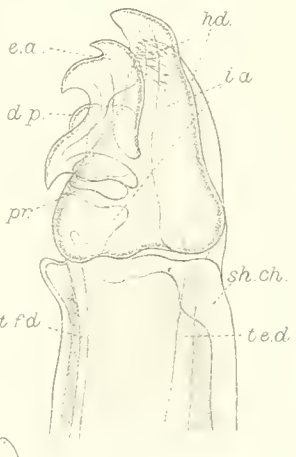

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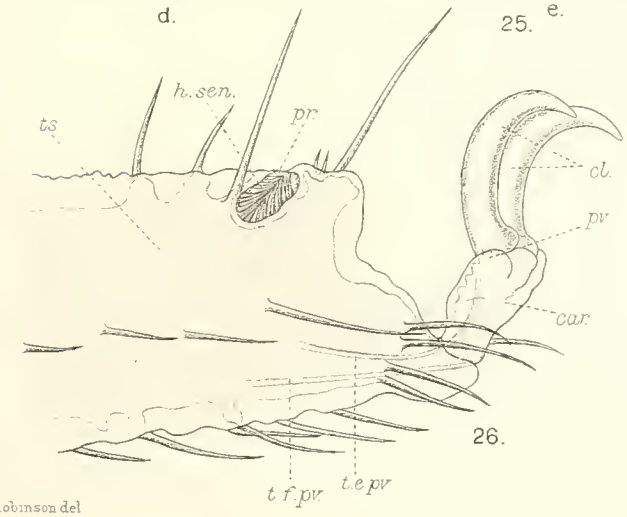

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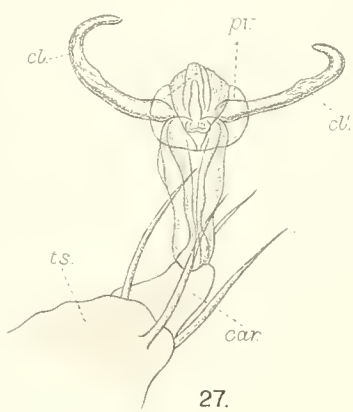

27.

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h.sen.	sensory hairs.
i.a.	internal article.
imp.m.	muscle impressions.
l.i, l.ii, l.iii, l.iv.	legs i to iv.
mac.	macula.
o.cx.gl.	external opening of coxal gland.
o.Gen.org.	external opening of Gené's organ.
o.ph.	pharyngeal orifice.
os.	ostium of spiracle.
p.	palp.
p.i, p.ii, p.iii, p.iv.	articles i to iv of palp.
p.d.m.	postero-dorsal margin of capitulum.
ph.	pharynx.
p.h.h.	post-hypostomal hair.
p.p.h.	post-palpal hair.
pr.	pore.
pts.	protarsus.
pv.	pulvillium.
sc.	scutellae.
s.ch.	outer sheath of chelicera.
s.ch'.	inner sheath of chelicera.
sc.m.	marginal scutellae.
s.cx.f.	supracoxal fold.
sh.ch.	shaft of chelicera.
sp.	spiracle.
st.	stomach.
sub.ch.p.	sub-cheliceral plate.
tb.	tibia.
tch.	trochanter.
t.e.d.	extensor tendon of digit.
t.e.pv.	extensor tendon of pulvillium.
t.f.d.	flexor tendon of digit.
t.f.pv.	flexor tendon of pulvillium.
tg.	tongue-like process above pharyngeal orifice.
ts.	tarsus.
v.b.w.	ventral body wall.

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NOTE ON COLOURATION IN TICKS.

By GEORGE H. F. NUTTALL, F.R.S.

(*From the Quick Laboratory, University of Cambridge.*)

(With Plate VII.)

The ornamentation so characteristic in *Amblyomma*, *Aponomma*, *Dermacentor*, and occasionally met with in species of *Rhipicephalus* and *Hyalomma*, is of use to the systematist in the differentiation of species. In many descriptions of ornate Ixodidae the colours are referred to as "metallic" owing to the sheen they possess when the ticks are preserved in alcohol.

Whereas many authors no doubt describe the colours as they are seen in specimens preserved in alcohol, others appear to describe them from dried specimens. The object of this note is merely to point out that authors should state in their descriptions whether the ornamentation is described from specimens preserved in alcohol or simply dried, and to enter a plea with workers in the field that they should, wherever possible, note the colours of *living* ticks.

The accompanying Plate (VII) will serve to illustrate my remarks. It is the very accurate work of Mr Edwin Wilson, based on camera-lucida drawings of my own, the colouration of the scutum being an exact reproduction of what is seen by daylight both in living and in well-preserved dried specimens of *Amblyomma variegatum* (♂ and ♀) and *A. splendidum* (♂). Thanks to the kindness of a correspondent in the Lower Congo, I have recently come into the possession of living specimens (N. 1650 and 1650*a*) of the foregoing species of ticks, the first, I believe, that have arrived in a living condition in Europe. In view of the beautiful ornamentation shown by the living ticks I could not resist the temptation to illustrate them.

It will be seen that the chief markings are retained in dried specimens and a comparison with ticks preserved in alcohol shows that

the latter also preserve the essential characters. The markings are lost, however, in specimens that are not adequately preserved soon after they die, this being doubtless due to putrefactive changes within the body of the tick. Collectors should, therefore, kill and preserve their specimens as rapidly as possible by placing them in 60% spirit or drying them. Formalin, whilst preserving the colours fairly well, has the disadvantage of rendering specimens brittle.

If we compare the colouration of *A. variegatum* ♂ when alive (fig. 1) and preserved dry (fig. 2) we see that the black markings turn brownish, the coppery markings yellow, and that a great deal of the brilliant green between the black and coppery markings is lost; the beady eyes change from black to pale yellow and they appear larger. It is worth noting that when dried specimens are placed in alcohol they, in a measure, resume the tints seen in living ticks, but the colours become "metallic" so that the light areas appear like burnished copper bordered by green possessing a metallic sheen; the eyes are pale and translucent and the black or blackish-brown of the living tick turns to a chestnut-brown. Corresponding changes are observable in the ornate scutum of the ♀ (figs. 3 and 4).

Similarly, if we compare a living and a dried specimen of *A. splendidum* ♂ (figs. 5 and 6), we see that the chief markings are retained, although the colours are altered. The beautiful pink colouration seen in most of the light portions, the pale green markings midway along the lateral folds, the white markings on eight of the festoons, all change to a pale yellow; the brilliant red central spot enclosing the two black dots which indicate the foveae, appears shrunken and dull; the emerald green lines bordering the black and the violet tint of the median part of the dorsum are replaced by a more general greenish colouration; the brownish lateral folds grow dull and the dull greyish eyes grow bright yellow. When dried *A. splendidum* are placed in alcohol they, as in *A. variegatum*, resume, in a measure, the colour seen in the living specimen, but the colours are metallic. The pink areas seen in the living specimens now assume a deeper coppery tint, the green becomes more intense and brilliantly metallic, the white markings on the festoons give off a light violet or green metallic reflection and the eyes appear pale yellow.

Corresponding changes take place in other ticks belonging to the genus *Amblyomma* and the subgenus *Aponomma*, the tendency for the ornamentation to give "metallic" colours, when specimens are preserved in alcohol, being especially characteristic in these ticks.

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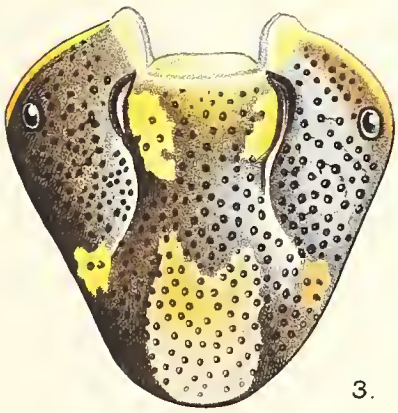

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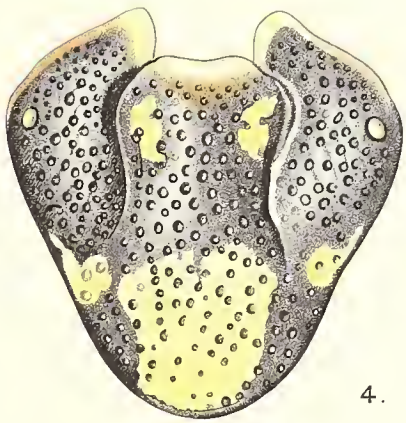

4.

5.

6.

Edwin Wilson del. Cambridge

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DESCRIPTION OF PLATE VII.

All the specimens were drawn with the aid of a Zeiss binocular dissecting microscope by daylight. Only the scutum of the ticks is shown in each instance. Figs. 1, 2 and 5 were drawn from specimens within about a week of their emergence from the nymphal skin on the journey from the Lower Congo.

Fig. 1. *Amblyomma variegatum* ♂, alive.
Fig. 2. ,, ,, ♂, dead and dried.
Fig. 3. ,, ,, ♀, alive.
Fig. 4. ,, ,, ♀, dead and dried.
Fig. 5. *Amblyomma splendidum* ♂, alive.
Fig. 6. ,, ,, ♂, dead and dried.

A SARCOCYST OF A GAZELLE (*G. RUFIFRONS*) SHOWING DIFFERENTIATION OF SPORES BY VITAL STAINING.

By ANDREW BALFOUR, C.M.G., M.D., B.Sc., F.R.C.P.E., D.P.H.
(*Director, Wellcome Tropical Research Laboratories, Gordon College, Khartoum.*)

(With Plates VIII and IX.)

In May 1912 when on the way with our Floating Laboratory to Rejaf, *en route* for the sleeping sickness district in what was formerly the Lado Enclave (now part of Mongalla Province), the late Colonel Mathias shot, near Renkwood station on the White Nile, two specimens of the Senegal or red-fronted gazelle—*Gazella rufifrons*. I found one of these animals, a female in good condition, heavily infected with sarcosporidiosis, the diaphragm, the intercosted muscles and those of the thigh being specially affected, though the striped muscle fibre everywhere contained cysts in varying numbers. In the light of the observations made by Probst and Francis (1910) the blood was carefully examined but no sarcosporidial spores were found in it nor were any blood parasites present.

I am not aware that sarcosporidial infection has hitherto been found in this species of gazelle though, as Teichmann (1912) states, it has been discovered in the stag and the roe-deer, while recently, Ross (1910) in British East Africa has described a sarcocyst in Grant's gazelle—*G. granti*. Hence, although it was not possible to carry out any extensive investigation of the condition, it seems desirable to give some description of the parasite and more especially to deal with certain observations made by the aid of vital staining with toluidin blue. In the first place it may be said that the muscle cysts or so-called "Miescher's tubes" which possessed fairly thick and tough walls measured,

on an average, 4 mm. in length and contained the usual spores or sporozoites lying in a milk-white and cheesy medium which could be easily smeared out upon a slide and contained what looked like minute crystals. The spores themselves, which in different cysts were at different stages of development, varied in shape and size in the living, unstained condition. Measured, when in normal salt solution, by means of a micrometer eye-piece, the crescentic forms were found to vary from 13 to 15 μ in length, and from 3 to 4·5 μ in breadth at their widest portion, *i.e.* the centre of the spore. Smaller spherical forms had a diameter of 8 μ. There were also present larger, very pale, spherical bodies containing granules and measuring about 13 μ in diameter. I cannot be certain that these were spores; they may have been examples of the pansporoblast stage of Doflein.

The crescentic or sickle-shaped spores, when stained by the Giemsa method, were found to measure from 15 to 16·5 μ in length, while the breadth at their widest parts varied from 3 to 3·5 μ. The stout, somewhat oval forms were usually 13 μ × 15 μ.

These measurements were first made by using the micrometer eye-piece; they were afterwards confirmed in Khartoum, employing Bruce's method of measuring drawings made at a magnification of 2000 diam. by means of a Greil's projection apparatus.

The description given by Ross (1910) of sarcocyst spores in the ox, which were indistinguishable from the spores contained in the large cysts found in Grant's gazelle, applies almost equally well to the spores in *G. rufifrons*.

It is as follows:

"There are two types, a sausage shaped or oval form and a more elongated form. The latter are distinctly more pointed at one end. The distribution of the chromatin is the same in both forms. At one end—the more pointed end in the long forms—there is a dense mass of chromatin completely filling the end, no protoplasm being visible between the chromatin and the edge of the parasite. At the opposite end is another mass of chromatin which is not, however, terminal. Protoplasm can be clearly seen all round it, and the appearance of the chromatin is quite different to that at the other end. The latter stains deeply and uniformly, the former takes a paler stain and has more deeply stained chromatin granules scattered throughout." In the case of the Sudan parasites (fig. 1) this latter chromatin, which consists wholly of scattered granules, lies in a clear, unstained area which stretches from side to side of the spore. The more elongated spore

forms in many instances are distinctly crescentic. Otherwise the above description serves very well, but the presence of vacuoles, sometimes single, rather large and central, sometimes small and in duplicate, should be mentioned. In addition to the two main types of spore, there were large oval or irregular shaped forms staining a homogeneous blue colour and each containing two separate masses of somewhat reticular or granular chromatin, sometimes separated from each other by the whole length of the spore and sometimes seen to be side by side. These suggested mother cells prior to division into spores, degenerated forms, or spores altered in shape by the spreading out of the cyst contents on the slide. They were fairly numerous in the smears and are shown in figs. 2 and 3.

In the case of spores stained by the Leishman method the chromatin of the polar cap was seen to be distinctly granular.

A very different appearance, however, was presented when vital staining with toluidin blue was employed in the manner I have already described (1912). This method quickly differentiated two very distinct forms of spore (fig. 6). One was stout, markedly more rounded at one end than at the other, took on a dark blue colour, especially at its centre, and in nearly all cases exhibited a large vacuole towards the more pointed end. This vacuole, which in some spores was very large, was not terminal and between it and the sharper end was an area of cytoplasm some of which stained as darkly as the central area of the spore. The cytoplasm at the blunt end tended to be lighter-coloured. The other form was distinctly of a crescent shape, and in many cases was very definitely crescentic, possessing pointed ends, one of which was, as a rule, a little blunter than the other. The cytoplasm generally stained a very pale violet colour, in marked contradistinction to the deep blue of the stout spores, and at, or near, the centre were grouped violet-coloured granules. In some instances the granules were found rather scattered throughout the spore cytoplasm. As regards size there did not seem to be much difference between these vitally stained forms. The measurements already given apply to them. Some of the stout forms were quite as long as the crescentic but looked shorter owing to their being thicker.

It is rather remarkable that it was only by vital staining that the above marked difference could be demonstrated. Very little is known about the life-history of the sarcosporidia and their study is by no means easy, but it is interesting to note that Minchin (1912) says that possibly there may be more than one kind of spore even in the same

species of parasite. This would certainly seem to be the case in the species under discussion. I found that successful permanent preparations of the vitally stained spores could be obtained by gently spreading out the fluid containing them on a slide and fixing by heat. The colour, however, soon faded. One would ask if it is possible that amoebulae of male sex might be derived from the crescentic spores and female amoebulae from the stout forms. There is no proof that this happens, but Minchin has suggested that sexual processes may take place between different amoebulae and it would be interesting to follow up this question.

Some of the cysts were dipped into spirit, then flamed and transferred to culture tubes of Nicoll's blood agar; the cysts were then ruptured, thus seeding the medium with spores. I also made broth cultures in the same way but was unable to trace any development. Many of the spores seemed quite unchanged after 44 hours at room temperature (about 33° C.). Some became spherical in the broth, and thus obviously degenerated. The only point possibly worthy of note was that in both lots of cultures a number of small, hyaline spherical bodies were found, many of which contained a dark, motile granule. These bodies did not take on the vital stain and I could come to no decision regarding them, though perhaps they were very young spores or possibly even amoebulae derived from them. It was not possible to carry out any feeding experiments with this *Sarcocystis gazellae* n. sp. (?), as I propose to call this sarcosporidian, although in the light of recent work by v. Betegh and Dorcich (1912) this may not be justifiable, for their researches tend to show that possibly the same species of sarcocyst may occur in a number of different species of animals and even indifferently in birds and mammals. Owing to the small size of the cysts it would seem to be a different species from that found in Grant's gazelle but this may not be the case. Ross does not appear to have given his parasite a name. Fig. 4 shows a section of a ripe cyst embedded in the muscle fibres. The wall of the cyst is quite distinct from the surrounding muscle fibre, from which however, as stated by Fiebiger, it may have been derived. Crescentic or sickle-shaped spores are found throughout the whole of the cavity of this cyst. They are arranged in definite clusters following the outlines of the chambers formed by what Doflein terms the "plasmareste." At the periphery of the cyst may be seen large round and undifferentiated cells which are the pansporoblasts or mother cells. They are better shown in fig. 5 which represents part of a section stained by Heidenhain's iron haematoxylin

method. In this case spores were only found close to the cyst wall. The greater part of the cavity was filled with a granular debris doubtless derived from the disintegration of degenerated spores (fig. 7). The chamber-forming network of the "plasmareste" is visible throughout; it is denser at the centre of the cyst.

I am indebted to Mr George Buchanan both for the drawing and the microphotographs.

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DESCRIPTION OF PLATES VIII AND IX.

Figs. 1 to 7. *Sarcocystis gazellae* n. sp.

Fig. 1. Free spores (×1000). Stained Giemsa.

Fig. 2. Ordinary spores and large binucleate type of mother (?) cell (×1800). Stained Giemsa.

Fig. 3. Ordinary spores and different type of large binucleate mother cell (×1800). Stained Giemsa.

Fig. 4. Longitudinal section through a cyst full of spores (×20). Stained Giemsa.

Fig. 5. Section of cyst, showing the cyst wall, peripherally placed mother cells, and spores lying in clusters in the cyst chambers (×640). Stained iron haematoxylin.

Fig. 6. Free spores, stained *intra vitam* by toluidin blue.

Fig. 7. Longitudinal section through a cyst, the greater portion of which contains no spores. Those present occur round the periphery (×20). Stained iron haematoxylin.

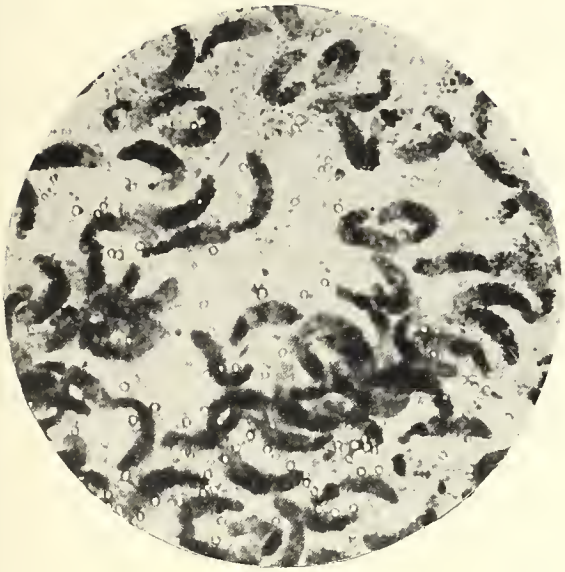

Fig. 1.

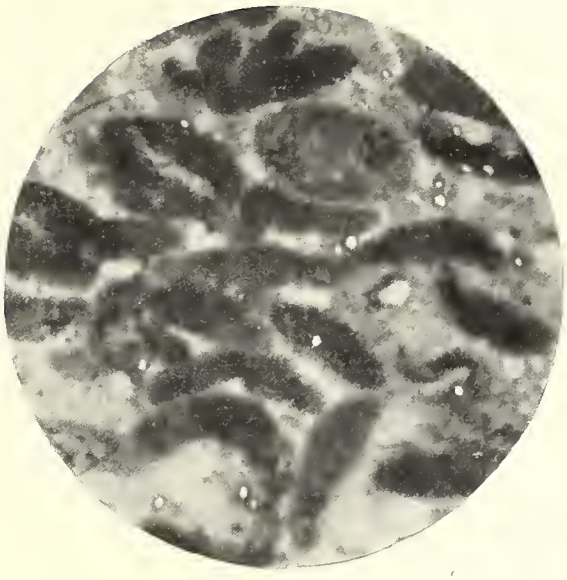

Fig. 2.

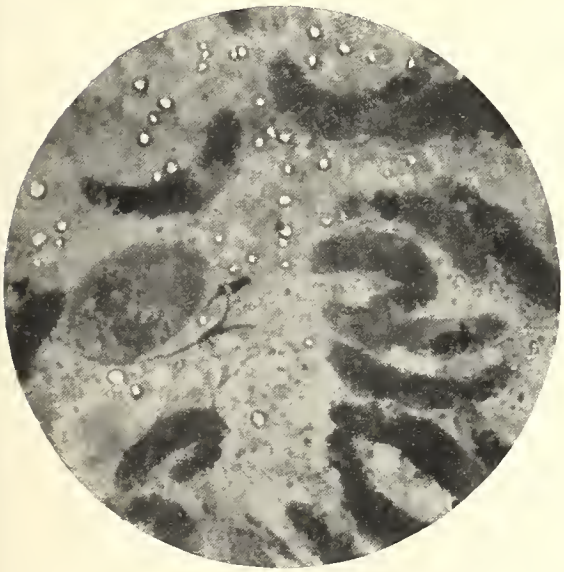

Fig. 3.

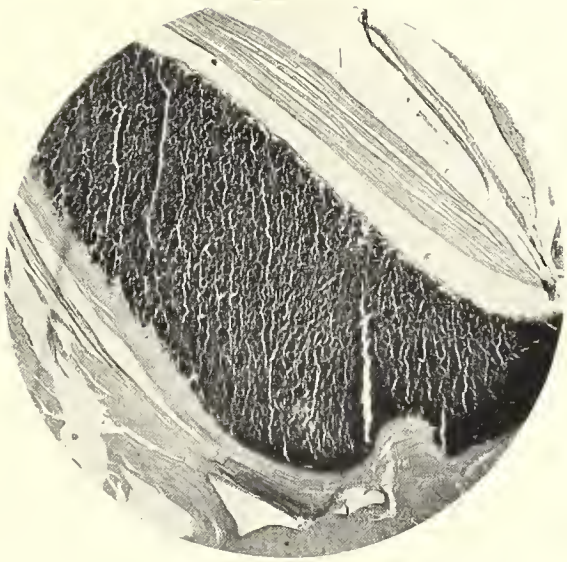

Fig. 4.

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Fig. 5.

Fig. 6.

Fig. 7.

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ANKYLOSTOMIASIS IN GRENADA.

By R. P. COCKIN, M.A., M.B., B.C.

(Thesis for M.D. Degree in the University of Cambridge.)

When, in June 1911, I took over the charge of the Colony and Yaws Hospitals at St George's, Grenada, I learned from the Medical Reports that ankylostomiasis was existent in the Colony—a dozen cases having been treated in the Colony Hospital for this disease during the previous year, and one case having been met and treated in one of the out-districts.

Upon enquiry I learned that some twelve years previously a Dutch Naval Surgeon, whilst visiting the island, had proved the existence of the disease; and at the same time had shown that the greater proportion of the cases then under treatment for malarial cachexia were in reality suffering from anaemia, the result of ankylostome infection.

Dr Boyd, who was at that time in charge of the Colony Hospital, took advantage of the information given and proceeded to treat all cases sent in to him as "anaemia" or "malarial cachexia" with vermifuges; and with good results. This treatment was carried out empirically, no microscopical examination of the blood or stools being done. One of Dr Boyd's successors also carried out the same treatment after the examination of the suspected specimens had been made; but it was generally held that the radical treatment adopted by Dr Boyd had practically succeeded in stamping the disease out of the Colony, and very little importance was attached to such few cases as from time to time presented themselves for treatment either at the Hospital or in the out-districts.

In consequence of the information which I received from the Reports, and from the other medical men whom I met, I took over the charge of the Hospitals with the belief that ankylostomiasis, although present in the island, was present to only a limited extent and that although

the disease ought not to be forgotten when making examinations, yet its presence need not be invariably assumed until the contrary had been proved with the aid of the microscope.

One fact, however, which caused me much perplexity when taking over the cases in the Hospitals was the unusually large number of patients who were suffering from some degree of dilatation of the heart. This, I was informed, was extremely common in the island and was explained by the heavy work which the labourers employed on the large estates in the interior of the island (which is very rugged and mountainous) were called upon to do. This explanation did not seem to me to be satisfactory, since when in charge of mountainous districts in both Cyprus and Southern Nigeria I had not noticed a similar state of things to exist; also I found that the disease was not absolutely restricted to estate workers in Grenada. This condition of the heart and the fact that there were in the Hospitals several patients suffering from an intermittent fever, which did not respond to quinine and in the blood of which I was unable to find either malarial parasites or filaria, led me to make investigations with regard to the cause of both these maladies.

From the examinations of the blood which I had already done, I was aware that a considerable degree of anaemia was usually present, and that eosinophilia was marked. I consequently commenced to examine films from the stools of these patients and found that the ova of *Ankylostoma duodenale* were constantly present. This led me to examine the stools of all the patients in the Hospitals, and I was amazed to find that over 80 % of them had the ova of this parasite present in their excreta. A systematic examination of the dejecta of all those subsequently admitted to the Hospitals was instituted, and the results obtained showed the widespread extent of the disease amongst all those connected with estate work and its especial prevalence amongst the labouring class. There was, however, a certain proportion of these cases which had never worked either on the estates or in the gardens usually connected with them; and several of the cases were of young children of three years of age and upwards. The number of cases examined in this series was fourteen hundred, and included representatives from every grade of society in the Colony, from every part of the island, and of every age—from young children of three years to old men of eighty-five.

In this series it was uncommon to find the *Ankylostoma* ova alone, the usual combination of parasites in a specimen being: *Ankylostoma duodenale, Ascaris lumbricoides,* and *Trichocephalus trichiurus.* In one

specimen, from a boy of nine years of age, five other parasites were also found.

The intestinal parasites which were found in the examination of the whole series were as follows:

Nematodes.

(1) *Ankylostoma duodenale.*
(2) *Ascaris lumbricoides.*
(3) *Oxyuris vermicularis.*
(4) *Trichocephalus trichiurus.*
(5) *Strongyloides stercoralis.*

Cestodes.

(6) *Taenia solium.*
(7) ,, (? *confusa*).

Protozoa.

(8) *Amoeba coli.*
(9) *Balantidium coli.*
(10) *Trichomonas hominis.*
(11) *Paramoecium coli.*

Insecta.

(12) The larval forms of two of the Muscidae—one of which was *Chrysomyia macellaria*, and the other being unidentified.

The percentage infection of the more common of these parasites is given in the following table:

A. duodenale	879 cases	62·78 %
A. lumbricoides	986 ,, ...	70·42 %
T. trichiurus	1083 ,, ...	77·35 %
O. vermicularis	149 ,, ...	10·64 %
S. stercoralis	196 ,, ...	14·00 %

It will thus be seen that *Ankylostoma duodenale* was present to the extent of 62·78 % of the sick population sent up for treatment at the Hospitals. Of these cases not two per cent. were sent in for treatment for ankylostomiasis; the greater proportion being sent in for intercurrent maladies having, I believe, no connection whatever with this disease. Upon looking up my cases I find that of the ulcer cases 75 % were infected, and of those suffering from yaws it was exceptional to find a patient who did not harbour the parasite. This relationship is extremely close, but only is so because these affections are commonest amongst the under-fed, under-paid, and badly-housed peasants who work upon the estates.

Of the cases of the series, which I found to be infected, not more than 45 % presented definite symptoms of the disease. The patients

usually complained of great weakness, pain in the epigastrium, or palpitation—either separately or in combination. The appearance of the patients was that of being well-nourished, the cheeks being fat and the body well covered. Puffiness under the eyes, pulsation of the great vessels of the neck and oedema around the ankles were, however, very frequently observed. Upon examination the conjunctiva was found to be oedematous and anaemic in proportion to the severity of the infection; in some cases this was very marked, in others no variation from the normal could be noted. The tongue was usually swollen, anaemic and indented by the teeth and the mucous membrane of the mouth was also anaemic. The bluish-black pigmented patches of which mention has been made by many observers were found to be present in 65 %; and this I found to be about the same percentage in which it occurs in other cases not affected with the disease. I am of the opinion that no connection exists between these pigmented areas on the tongue and ankylostomiasis. The epigastrium was generally found to be painful on pressure and pulsation of the epigastrium was common in advanced cases of the disease. The heart, in approximately 20 % of the cases, was found to be enlarged towards the left; sometimes being just outside the nipple line, at others being as far out as the mid-axillary line. Haemic bruits were usually found to be present in these cases; but, in advanced cases of the disease, mitral regurgitation was frequently noted. The rate of the heart beat is usually found to be normal and regular when the patient is at rest; but on the slightest exertion, as in getting up from a chair, the rate is at once accelerated. Nothing abnormal is usually noted in the lungs; but those cases, which through their extreme weakness and disability have been compelled to remain in their beds, generally have some oedema at the bases.

The liver was generally found to be normal, but in some 5 % of the cases slight enlargement was present. Occasionally the enlargement is extreme and in my series two such cases were observed, in which the hepatic enlargement extended down to within two inches of the umbilicus, and there was considerable ascites. Both these cases died.

The kidneys were not palpable in uncomplicated cases and the spleen was only made out in those cases which had previously had malaria. Examination of the urine showed the presence of albumen in 14 % of the cases infected with the parasite. In no case was I able to demonstrate the presence of albumose. My experience differs entirely from that of those observers who find that albuminuria

only occurs at a late stage of the disease ; since I found it to occur as frequently in early, as in late cases.

With regard to the connection which exists between infection with this parasite and the albuminuria and cardiac dilatation so frequently found associated with its presence, I made notes on a consecutive series of 172 cases in which one or both these symptoms occurred. The results were as follows :

Albuminuria.		
(*a*)	Associated with ankylostomiasis	52
(*b*)	Not ,, ,, ,, ...	9
Cardiac dilatation.		
(*a*)	Associated with ankylostomiasis	70
(*b*)	Not ,, ,, ,, ...	2
Albuminuria and cardiac dilatation.		
(*a*)	Associated with ankylostomiasis	37
(*b*)	Not ,, ,, ,, ...	2

From this table it will be noted that whereas in 159 cases of the series the parasite was found to be present, it was only absent in 13 ; in other words the association was one of 92 %, a percentage out of all proportion to the degree of incidence which we know to obtain amongst the sick population generally.

These results also disprove the theory that prevails with regard to the causation of the cardiac dilatation being the result of arduous labour in a hilly country. The hills undoubtedly play a part, but only that of aggravating an already diseased organ, not of causing the disease.

A series of twenty-five blood examinations was also made from the members of this series, and the results obtained are tabulated below. I should, however, state that all the specimens examined were taken from cases in which the disease was advanced and the anaemia extreme.

The average of the counts was as follows :

Red cells	1,265,000
White cells	10,000

and the average percentage of haemoglobin was 20·5.

The differential leucocyte count was as follows :

Polymorphonuclears	49·5 %
Eosinophiles	22·4 %
Lymphocytes	15·8 %
Mononuclears	7·6 %
Other forms	4·7 %

No nucleated red cells were seen in any of the films which I examined and megalocytes in only three of the cases. Poikilocytosis and polychromasia were each observed in two specimens. The blood obtained for examination was always pale in colour and abnormally fluid. The red cells displayed no variation in colour and were uniformly pale.

I am unable to agree with those observers who state that the blood of natives suffering from this disease more closely resembles that of patients suffering from pernicious anaemia, whilst that examined from cases of the disease in white subjects approximates more closely to that seen in cases of chlorosis. The above results were all obtained from specimens taken from either negroes, coolies or patients of African descent, and vary little, if at all, from those obtained by Haldane and Boycott as the result of their observations on Cornish miners.

A history of ground-itch was given in 93% of the cases and this percentage would, in all probability, have been larger had one been sufficiently well acquainted with all the languages spoken in the island.

With regard to the intermittent fever mentioned at the commencement of this paper I am unable, at present, to say more than that its presence is inconstant and that it is not dependent upon the severity of the infection. I found that all the febrifuges employed were useless in reducing the temperature and that the only method which succeeded in accomplishing this end was treatment with one of the drugs that brought about the expulsion of the parasites.

One of the commonest of the complaints made by patients suffering from this disease is that of constipation, but it occasionally happens that the complaint made is that of diarrhoea, associated with the passage of blood and mucus. In consequence, many of these patients are sent up to the Hospitals for treatment for dysentery. One such case, who complained of having had this distressing trouble for several years, was found to harbour many of these parasites and the expulsion of these was followed by complete cessation of the trouble for which he was admitted. In this case I was unable to find any amoebae upon the examination of the stool, and my attempts to isolate *B. dysenteriae* were also negative. This patient reported himself as "well" a year after his discharge from the institution, and I can come to no other conclusion than that the dysenteric symptoms were caused by the presence of *Ankylostoma duodenale* alone.

The treatment of ankylostomiasis resolves itself into:

(1) That directed to the removal of the parasites.

(2) That needed for the effects produced by their presence.

(1) With regard to the removal of the parasites I have had experience of four methods of treatment; only one of which I consider to be quite satisfactory.

In testing the drugs at my disposal I took three series of fifty cases each; the members of the first series were treated with thymol, those of the second with eucalyptus oil, castor oil and chloroform, and of the third with beta naphthol. In consequence of the excellent results obtained with this latter drug a fourth series with male fern was not completed; since in eleven cases, in the treatment of which this drug was used, recourse to one of the other three had to be made in order to complete the expulsion of the parasites. The results obtained from these three series of cases varied greatly and the deductions drawn from them are briefly as follows:

(*a*) *Thymol.* This drug if given in full doses of thirty grains is dangerous, if in smaller doses it is not effective, for when given to a fully developed man in twenty grain doses, it occasionally took as long as a month to rid him of the parasites. It not unfrequently happened that even when the parasites had ceased to appear in the motions the ova were found upon microscopical examination of the stool. My experience of this drug teaches me that it is very dangerous in cases of cardiac degeneration, and I do not think that it should be used in any case where this condition is found to exist to any degree. For this reason I consider that the method of free distribution of thymol, adopted by the Porto Rico Commissioners, is very dangerous; since, from my work in Grenada, I know that a large percentage of these cases must be suffering from dilatation of the heart in varying degrees, and the carelessness of the West Indian native in attending to instructions is proverbial.

(*b*) *Eucalyptus Oil, Castor Oil and Chloroform.* This series of cases was the most disappointing of the three, and in thirty-eight cases of the series it was necessary to administer either beta naphthol or thymol to complete the removal of the worms. No ill effects were noted as attending its use.

(*c*) *Beta Naphthol.* The results obtained from the cases in this series were most satisfactory, and convinced me of the superiority of this drug. As I have continued its use upon all subsequent cases of the disease I have had ample opportunities of confirming the opinion which was then formed with regard to it. The points in favour of beta naphthol are its rapid and complete expulsion of the parasites, the absence of danger attending its use and the relatively small cost. It

was unusual for a patient to require more than three administrations of the drug, and it not rarely happened that one day's treatment was sufficient to completely expel the parasites. No ill-effects followed its administration to either parturient women, or to children. The only complication ever noticed was that of haemoglobinuria, and this occurred in five cases of the patients treated with beta naphthol; about 1 % of the cases. Of these five cases, three were males and two females. On each occasion the drug was stopped at once and liquid extract of ergot in half-drachm doses substituted. In four cases the haemoglobinuria ceased within forty-eight hours, and in the fifth the urine was clear on the third day. In these cases, after a few days' rest, treatment was continued with thymol without recurrence of the renal symptoms.

It is advisable in all cases where treatment for the removal of these parasites is being carried out, to re-examine the stools for ova after worms have ceased to appear in the motions; since *Ankylostoma duodenale* seems to acquire an immunity to a drug after a certain period of treatment. In these cases, where ova are found upon re-examination, I found it advisable to change the vermifuge altogether; as continuance with the one which I had been using previously was ineffective. This immunity of the parasite to a drug may happen in the case of any of those which I used, but most frequently happened in the case of thymol.

(2) With regard to the treatment of the heart it was generally found advisable, where marked dyspnoea, palpitation, or irregularity of the pulse was present, to give the patient a course of digitalis before commencing treatment for the removal of the parasites; and to continue its use on alternate days until treatment with beta naphthol was finished.

The treatment for the anaemia was carried out subsequent to the removal of the parasites, and was generally very prolonged. Convalescence in Hospital on a liberal diet and the administration of a mixture containing iron, arsenic and strychnine gave the best results. Recovery from the anaemia was slow and it is generally some months before the normal haemoglobin percentage is regained.

When the ascites is marked, in those cases with hepatic enlargement, tapping may be frequently needed. I found that neither the pyrexia nor the albuminuria called for special treatment; since removal of the worms was followed by cessation of these symptoms in all uncomplicated cases.

Suggestions as to the measures to be taken to free the Colony from the disease.

(*a*) Since the greater proportion of the patients were employed in work on the estates, it is justifiable to assume that the estates are the ordinary foci from which infection in the Colony arises, and consequently it is to the estates that attention should first be turned.

The first point which calls for attention is the latrine accommodation on the estates, both in the fields and also in connection with the labourers' cottages.

At present this is either non-existent, or present only in isolated instances. Thus one estate which I visited and which employs considerably over a hundred labourers was not furnished with a single latrine, with the exception of the one supplied for the use of the overseer. This estate is notorious for the anaemic condition of its workers and some of the worst cases of the disease which I have seen came from this place. It was on this estate that I was informed that ground-itch was more common there than in any other part of the island; in consequence, probably, of the widespread infection of the ground.

Destructors for the incineration of the contents of the latrine pans could be erected at a small cost, and in my opinion this would be preferable to the trench system.

(*b*) Since most of the infection is received from the ground the use of boots whilst working on the estates should be compulsory. I am informed that where indentured labour is used on estates, as in British Guiana, the labourers, when going to the fields in the morning, are made to walk through a tank containing a tarry composition. This procedure attains the same end as the wearing of boots; but since the natives of Grenada refuse to submit to this form of protection, the wearing of boots is the only alternative.

(*c*) The infected ground of the estates would need treatment by the application of lime. This would require forking in thoroughly and could be done at the same time as the trees were being manured.

(*d*) In view of the difficulty of detecting recent deposits of excreta on the ground it is advisable that spaces be left between the rows of trees. This is, I believe, compulsory in some colonies and has been proved not to affect the yield from the estates.

(*e*) Proper drainage of the estates is also an important measure; for it is in the dank, warm soil under the shelter of the trees that the ideal conditions for the development of the larvae are obtained.

(*f*) The institution of dispensaries for the free treatment of this disease and the free distribution of drugs is also an essential measure for eradicating the parasite from the Colony.

The best drug, in my opinion, for distribution in this way is beta naphthol in the form either of pills or in mucilage. In cases where the estate was situated too far from one of the dispensaries, a free supply of the pills, with instructions as to their administration, could be issued to the overseer or manager for the use of the labourers. I cannot too strongly emphasise the responsibility of the estate owners in this matter; since, at present, the whole of the legislation of the Colony is in their hands. I am confident that the adoption of these or similar measures could entirely rid the island of the disease; and at the same time lessen the mortality of the island to at least one half its present proportions.

Even from an economic standpoint the cost of these measures would be saved many times over; for the loss of time from sickness, the cost of maintenance and treatment in the Government Hospitals, and the natural shortage of labour and increase of wages resulting from the disease, would be avoided.

The methods of administering the various vermifuges mentioned in this paper were as follows:

(*a*) *Thymol.* The patient who was to receive this drug was put on to a milk diet for twenty-four hours previous to administration. The bowels were opened at 6.0 p.m. of that day with a saline aperient. At 6.0 a.m., the following morning, thymol gr. 20, in cachet form, was administered and at 8.0 a.m. the same dose repeated. At 12.0 noon a saline aperient was again given and the resulting motions saved and washed.

(*b*) *Eucalyptus Oil, Castor Oil and Chloroform.* As in the thymol method the patient to receive this drug was put on to a milk diet the day previously and was similarly given a saline aperient the night previous to administration. At 6.0 a.m. an emulsion containing Ol. eucalypti m. 15, chloroformi m. 20 and Ol. ricini dr. 5 was given; this was repeated at 7.0 a.m. The resulting motions were collected and washed, and examined for parasites.

(*c*) *Beta Naphthol.* In the case of patients who were to receive this drug the ordinary Hospital diet was given on the day previous to treatment. At 6.0 p.m. a saline aperient was administered and no more food was permitted that day or on the day of treatment, until the motions from the action of the beta naphthol were obtained. At 6.0 a.m. beta naphthol gr. 30 was given in mucilage and this was repeated at 8.0 a.m. and again at 10.0 a.m. At 12.0 noon a saline aperient was given and the motions resulting were collected, washed and examined.

OBSERVATIONS ON THE BIOLOGY OF IXODIDAE.

PART I. DEALING WITH

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(With 2 Text-figures.)

Introduction.

The observations on the biology of ticks which form the subject of this paper were made in the course of the last few years in Cambridge. In several instances (*Haemaphysalis leachi, Ixodes ricinus, Rhipicephalus appendiculatus*), the ticks were raised in connection with experiments upon piroplasmosis in dogs and cattle. The main facts regarding some of the species of whose life histories this paper treats are already known: *Ixodes ricinus* for instance is dealt with in *Ticks*, Part II. pp. 294–315; *Haemaphysalis leachi* has been studied by Lounsbury and Nuttall; *H. punctata* by Nuttall, Cooper and Robinson, and more recently by Stockman; *Rhipicephalus appendiculatus* by Lounsbury; whilst *Hyalomma aegyptium* has received but little attention. In none of these cases are the published records of such a nature as to complete

our knowledge of the life histories of the species, and the records are as a rule wanting in essential details and precision. Although all the data required have not been collected it appears desirable to publish these observations as they stand. An attempt has been made to make the records as complete as possible and to arrange the material in a uniform manner, so that certain data can readily be found by reference to the protocols. Of the remaining species, *Ixodes putus, canisuga* and *hexagonus*, little or nothing has hitherto been known regarding their biology. Wherever the work of other authors has been cited, full credit has been given them for what they have accomplished; in some cases a note incorporating all the information contained in their papers is given.

It is essential that ticks should be raised experimentally, not only that we may become familiar with their behaviour as parasites but with the part they play in pathology. The future will show that it is only by raising them under laboratory conditions that we can determine their degrees of variation in structure and learn to be familiar with their immature stages. At present the systematist can scarcely recognize more than a few immature forms of well-known species and undoubtedly differences due merely to individual variation have led to the creation of bad species.

Methods.

It may be useful to other workers to know about the methods we have employed for raising ticks.

Infesting the host and collecting replete ticks. When cattle were used as hosts the ticks were most commonly placed upon the ears, the latter being enclosed in bags. A bull would have been more convenient, the bag being placed about the scrotum. A ram has been used repeatedly for feeding ticks upon the scrotum, the replete ticks falling into the bag when they abandon the host. When ticks attached themselves in other situations, either on cattle or sheep, we had to rely on chance for their recovery in a stall which was kept as clean as possible. When dogs or the jackal served as hosts they were placed in specially constructed metal cages shaped like a barrel placed horizontally upon an insulated stand, one end of the barrel being open but guarded by a metal grating; a similar grating served as a floor for the animal to stand upon. Smaller animals were placed in appropriate metal cages standing in large whitened trays, around the outer margins of which there was a gutter filled with water. By cleaning and inspecting the cages

frequently the ticks could be readily found after they had dropped from the host—sheets of white paper, frequently renewed, have usually been laid upon the floor of the cage immediately beneath the grating upon which the host animal rests. The cages were searched for ticks at least once daily whilst gorged specimens were dropping from their host, and their numbers, etc. were on each occasion noted immediately.

In cold weather, before infesting the host, it is sometimes necessary to activate hungry ticks by warming them in a thermostat, for cold renders them torpid. After all, as Stockman has pointed out, warming the ticks in this manner is but to simulate conditions which may arise in nature when a warm-blooded animal rests upon tick-infested ground in cool weather and activates the ticks through the warmth radiating from its body.

Maintaining ticks apart from the host. When gorged larvae and nymphs had been collected from the floor of the cage or elsewhere, they were placed in wide-mouthed bottles or inverted bell-jars containing a layer of dampened earth an inch or so in thickness. The surface of the earth was pressed smooth, and folded pieces of filter paper were laid upon it for the ticks to creep upon. The aperture of the vessel was guarded with fine-meshed muslin held in place by rubber bands and string or thread wound around the vessel and knotted. The ticks, when necessary, were periodically transferred to clean quarters. Gorged females were usually placed singly in wooden pill-boxes bearing numbers and dates, the boxes resting on a layer of slightly dampened earth in an open jar. After oviposition was nearly completed, the egg mass laid by each tick was placed in a tightly corked tube containing slightly dampened filter paper. In some cases isolated females were allowed to oviposit in similar tubes and their bodies were removed after death, the eggs remaining undisturbed in the tube during metamorphosis. It is best to moisten the filter paper or earth with 15 % NaCl solution for the first time, adding simply water afterwards if more moisture is needed. The addition of salt is a safeguard against moulds which formerly were a source of much trouble to us.

When dealing with active larvae it has been found at times convenient to keep them, both before and after hatching, in wide-mouthed bottles closed by a cork or glass stopper covered with filter paper. By moistening the filter paper which protrudes between the stopper and the mouth of the bottle a slight amount of water may be allowed to flow in and dampen the filter paper which covers the stopper within the bottle. In all cases an excess of moisture must be avoided; at times it

is unnecessary to dampen the atmosphere within the tick containers. A bright light is inimical to ticks; we have usually maintained them in semi-darkness in a glazed and curtained cupboard or in vessels covered by a cloth. By the use of thermostats the rate of development during metamorphosis may be greatly accelerated.

Keeping records. It is imperative to keep proper records relating to the ticks under observation and such records are best kept in tabular form with headings like those contained in this paper. By the use of headings to ruled columns relating to specific observations and the dates of certain occurrences, it is easy to guard against a regrettable oversight which cannot afterwards be remedied. As a matter of routine my laboratory assistant, Mr Clarke, makes a daily inspection of the whole stock of ticks under observation and makes notes in the protocols wherever necessary. By the use of narrow columns and short headings thereto the record of almost the whole life cycle of a species can be compressed into a single sheet of foolscap. It is owing largely to improperly kept records that there is such a dearth of information about the life histories of species of ticks which have been repeatedly raised by various observers. In place of the dates entered in the original protocols the number of *days* which have elapsed (let us say for metamorphosis) should be entered in any published results, for it is scarcely fair to the reader that he should have to calculate the length of the period from a confused mass of dates.

A complete record, when obtainable, should contain the following data:

(1) *The time the tick remains upon the host,* from the date it was placed upon it until it drops off gorged. The kind of host should be mentioned and the temperature at which it is maintained; the object of noting this is to determine if ticks remain longer upon the host in cold than in warm seasons. We lack information on this point. The record should contain data relating to larvae, nymphs, females and males, and their behaviour on different hosts.

(2) *The behaviour of the sexes either on or off the host,* together with notes on *copulation.* It has been noted, for instance, by Lounsbury for *Amblyomma hebraeum* that females of this species will not remain upon the host unless the males have previously attached themselves. At present I have *Amblyomma variegatum* under observation wherein the males are still attached to the host, over four months having elapsed since the females dropped off gorged. In most cases however males and females remain upon the host when placed thereon simultaneously. In a number of *Ixodes* the males do not attach themselves to a host

but seek the females in the hosts' burrows or nests where the females drop off gorged and the males undergo their metamorphosis from nymphs.

(3) *The time required for metamorphosis* from stage to stage: egg to larva, larva to nymph, nymph to adult, under varying conditions of temperature, etc.

(4) *Oviposition*: the time which elapses before the female begins to oviposit; the time required for oviposition; the number of eggs laid by single females.

(5) *Longevity* of the larvae, nymphs and adults when maintained unfed under stated conditions of temperature and moisture.

(6) *Part played in pathology* if ascertainable: in the transmission of disease and through the effects of their bites.

I am fully aware that some of my records are deficient in certain particulars; it has been found impossible for instance to raise certain species under experimental conditions. With regard to copulation the process has been observed in *Argas*, *Ornithodorus* and *Ixodes*, but not to my knowledge in any other genus. From the data comprised under some of the above headings, however, it will be possible to conclude how long a given species will take to complete its life cycle, beginning say on the day when the first eggs of a generation are laid to the day when the first eggs of the second generation appear.

That observations in the laboratory require to be supplemented by others carried on in the field is self-evident. Field observations are, however, not readily carried out except in tick-infested countries. A fallacy which may arise from laboratory experience alone concerns for instance the supposed length of time required for the completion of the life cycle. We know that ticks have great powers of fasting in the absence of a host and that they may hibernate. The time required for the completion of the life cycle may therefore vary considerably and be much prolonged under unfavourable conditions. In the summary at the end of the sections dealing with each species mentioned in this paper, I have given the time which the species requires to complete its life cycle under the favourable conditions of laboratory experiment. In nature, no doubt, this period is in the majority of instances more or less considerably prolonged.

In the course of our raising experiments, we have noticed that the records of "the time the ticks remain upon the host" are open to a certain fallacy in that some ticks do not immediately proceed to feed upon the host; this holds more particularly for what we have observed

in immature ticks. Such ticks at any rate may run about on the host for some days before they attach themselves and proceed to feed. We have observed this especially with regard to *Rhipicephalus bursa*, regarding which I shall report in a future paper. This behaviour will account in some cases for the prolonged period which elapses before the ticks engorge and abandon the host. The shorter periods recorded for the stay upon the host are therefore more to be relied upon in determining the period of parasitism. The seat of attachment of the tick upon the host may markedly influence the period of parasitism according to the blood supply of the host's tissues at the spot where the tick introduces its mouth-parts. If the tick only imbibes serous fluid or lymph it may remain attached to the host considerably longer than when it sucks blood.

The longevity observed in Ixodid ticks kept in corked tubes in the laboratory will certainly be found to exceed that under natural sur-

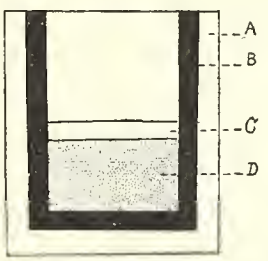

Fig. 1. Apparatus used for counting the number of eggs laid by a tick.

roundings. These observations nevertheless possess a certain value since they indicate that certain species are able to live for very considerable periods without food and that they have to be guarded against from this point of view in the practical work of eradication.

The number of eggs laid by individual females was determined by means of a simple little apparatus which I devised for the purpose and which is represented in Fig. 1, one quarter its natural size: *A* is an ordinary piece of glass, *B* three strips of glass cemented upon *A* in the form of the letter U between the arms of which *C*, a strip of glass, slides readily backward and forward whilst closely applied to *B*. The stippled surface *D* represents a single layer of eggs spread upon the glass between the frame *B* and the glass strip *C* which has been pushed downward to the point where the layer of eggs completely covers the quadrangular stippled surface which, as adjusted in the figure, represents about

10,000 eggs. By counting the number of eggs along two sides of the square and multiplying the figures we obtain with a considerable degree of accuracy the number of eggs which covers the area[1].

When enumerating by this method, we separate the eggs composing the mass by immersing them in normal salt solution and rubbing them about gently with the aid of a fine camel's hair brush. When the eggs are fairly well separated they are transferred with some of the fluid into the frame of the apparatus and the slide (*C*) is put in place. The eggs are now spread in a single uniform layer over the stippled area as shown in the figure, this being readily accomplished with the aid of a fine brush after draining away the superfluous fluid with a piece of filter paper. The eggs are readily ranged closely side by side like marbles. The counting can be done under a low power.

IXODES PUTUS.

The ticks (N. 1307)[2] upon which the following observations were made were collected by me in large numbers on 2. VII. 1911 about the nests of guillemots at Worm's Head, Gower, Glamorganshire, South Wales. The nests were situated in caverns and hollows in the rock upon precipitous cliffs, and access thereto could only be gained by descending from the brow of a cliff by means of a rope. A single bird's egg usually lay upon the damp mud which covered the rock. The ticks were found in all stages excepting that of unfed larvae. The engorged larva was described and figured by me in an earlier paper (*Parasitology*, v. p. 60). Whilst collecting specimens among the rocks a great number of unfed females of *I. putus* were captured upon the exposed rocks and the clothing of myself and my companion. No other stages were found wandering about. Only about a dozen adult males were captured and all of these were found either *in copula* or in close proximity to gorged females which were hidden in small hollows in the mud beneath loose stones; twice I found a couple of males together, the one *in copula*, the other waiting alongside the female. A single dead and shrivelled female was found beside a mass of eggs, likewise lying hidden in a muddy cavity beneath stones and aggregations of gorged larvae; unfed nymphs and replete nymphs

[1] Eggs do not suffer from the manipulation incidental to counting, the larvae hatch out within the usual period and are normal.

[2] On 4. VII. 1912 a second lot (N. 1703) was collected for me in the same place. The description of the adults and nymphs will be found in *Ticks*, Part II. pp. 256–261; it is accompanied by figures. The little hitherto known of the biology of this species is described on p. 317.

were found in similar situations. As the ticks were surrounded by mud constantly moistened by spray from the sea and scattered about by the birds returning from the water, I sought to maintain them, as far as possible, under natural conditions in the laboratory by placing the ticks in corked tubes containing the mud, or, better still, filter paper moistened with salt water, the tubes being kept in the dark or in a slightly darkened chamber. The salt prevented the growth of mould and it has since been found of use for the same reason in connection with the raising of other species of ticks.

Observations on living specimens.

The published descriptions of *I. putus* are based upon preserved specimens. It, therefore, appears desirable to record my observations upon the living tick without, however, repeating the detailed description of its external structures, regarding which the reader is referred to *Ticks*, Part II. pp. 256–261.

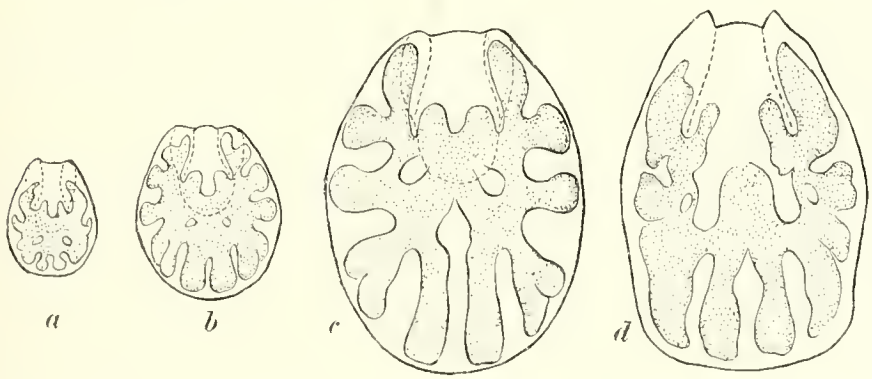

Fig. 2. *Ixodes putus*, showing the arrangement of the intestinal caeca in unfed living ticks, the digestive organs being viewed through the transparent dorsal surface. Dotted lines indicate the contour of the scutum and cervical grooves in the first three stages and the cervical grooves in the male. (*a*) Larva 87 days, (*b*) nymph 6 days, (*c*) female, and (*d*) male 14 days after ecdysis. The ticks grow somewhat paler in general body colour after hungering for some time owing to the contraction of the caeca following upon their having become partially emptied.

Male. During the first 24 hours after the young male issues from the nymphal skin its ventral surface appears slightly convex; viewed dorsally, the body appears dark owing to the material which occupies the still distended gut; pale areas between the folds of the gut are visible in positions corresponding to the cervical grooves and dorsal pits or grooves (Fig. 2 *d*). The legs and capitulum are a pale translucent yellow, the spiracles creamy. After 48 hours, owing to the intestine

having been partially emptied, the clear areas above described appear broader. The chitin has darkened somewhat, and the posterior portion of the "median plate" is clearly seen to be tegumentary (not hard) and pale; the hypostome and its base have now taken on a dark orange tint. After the fifth day the palps appear markedly darker distally. Whereas the tick is very sluggish in its movements during the first days after ecdysis, it moves about actively by the sixth day; the legs now appear darker and yellowish, the gut is much more contracted, and the stiff white hairs protruding from the posterior margin of the body[1] are frequently seen to be soiled by black excrement which forms ink-like spots when voided on filter paper. The base of the hypostome is now reddish-yellow in colour.

As the male ages, the body becomes concave ventrally, the pale areas become still broader, and the posterior part of the scutum curves more abruptly toward the venter so that the ventral plates project considerably. The distal portions of the palps and the moveable articles of the legs acquire a granular greenish colour especially on the ventral side. The yellow-coloured median plate is now seen to extend only two-thirds the distance between the sexual aperture and the anterior margin of the anal plate[2].

Female. The body of the freshly emerged female appears well filled, the legs pale, etc., as in the male. After 72 hours the base of the hypostome has acquired a distinctly orange-red tint, the tips of the palps are bluish, the legs begin to harden and show yellow and black dotted banding; although the intestine has been partly emptied it would seem as if the female does not void excrement as quickly as does the male after ecdysis. After 4–5 days the gut caeca are clearly distinguishable (Fig. 2 *c*), palpal articles 2–3 are bluish and translucent, the distal portions of the articles of the legs show annulations having a bluish tint, the ventral surface of these articles being a translucent orange-yellow. This colouration of the legs is maintained until the tick dies. The hypostome and its base is of a bright orange-red colour, the spiracles are milky with a large orange-red macula. All

[1] In one of the males a malformation was observed in that the tuft of hairs was absent on the posterior margin of the anal plate.

[2] This is contrary to what has been described hitherto, because in preserved specimens the line of demarcation between the hard median plate and the membranous integument posterior to it is indistinct. *I. putus* is the only species of *Ixodes* at present known where the median plate does not cover the whole surface bounded by the ventral grooves, anal and adanal plates.

the chitinous exoskeleton remains translucent. The body of the tick is now greyish, with a brownish scutum having dark lateral fields. After 8–9 days the appearance has altered little, the gut is more contracted, the palps and base of hypostome are more intensely coloured and the black and orange-red markings on the legs are more distinct.

In replete females the only change observed affects the body, which assumes a slate-grey opaque appearance.

Nymph. The freshly emerged nymph is sluggish; it possesses a black body and pale glassy legs which, after 24 hours, acquire a dull straw colour, whilst the intestine proceeds to partially empty itself. After 48–72 hours the nymph grows livelier, the gut is more contracted, the hypostome and legs are darker. After 5–6 days the capitulum and legs show the same colouration as in the female, the palps being, however, only slightly bluish distally; the intestine has been further emptied (Fig. 2 *b*), and the tick runs about actively. When replete, the nymph's body assumes a light slate-grey colour.

Larva. The larva of *I. putus* was described by me from replete specimens (*Parasitology*, v. p. 60) collected in 1911. Last year (1912) we fortunately succeeded in obtaining larvae from eggs which were laid by females (Lot 1703) in the laboratory. There is nothing material to add to the specific description of the larva, but it may be noted that unfed larvae are exceedingly pale and translucent, resembling recently emerged *Argas persicus* larvae in this respect. The arrangement of the intestinal caeca is shown in Fig. 2 *a*. In specimens that had fasted for some time two broad and shallow depressions are seen to run longitudinally along each side of the dorsum, the middle of the dorsum being convex and the body margins somewhat raised. When alive and at rest, the body of the larva measures, on an average, 0·55 × 0·45 mm.; the larvae, however, show some variation in size, as will be seen from the appended measurements of ten larvae picked out because of apparent

Larva No.	Length	Width
1	0·53 mm.	0·44 mm.
2	0·54	0·45
3	0·55	0·45
4	0·55	0·45
5	0·55	0·45
6	0·55	0·38
7	0·55	0·46
8	0·58	0·45
9	0·60	0·43
10	0·60	0·43

differences in size from a batch of about 100 belonging to one family. The smallest larva measured 0·53, the largest 0·60 mm. in length, the variation being as 88 : 100.

Changes in colouration at death.

On dying, the ticks usually turn blue-green all over, the bluish annulations on the legs becoming very dark. At first, the limbs assume the same bluish tint exhibited by the palps in living adults, the limbs then gradually darken and the colour spreads all over the body. It would be interesting to determine the cause of this change in colour. In Neumann's description of *I. putus* this blue-green colour is referred to as if it were natural; this is, however, not the case. To my knowledge, no similar change of colour occurs in other ticks when they die.

Feeding experiments.

Males. All attempts to make the males feed upon a host (duck, sea-gull, fowl) failed utterly. About 15 males of various ages were repeatedly tried on a fowl and 12 males on a gull and duck.

Females. Out of 15 unfed females which were placed upon a fowl, five attached themselves to the host after some patient waiting; all of them died *in situ* after about three days and, soon after they died, they assumed an olive-green colour similar to that of ticks which die unfed. The dead ticks rapidly grew dry and brittle and remained in this condition attached to the host and gradually fell to pieces.

I next tried the ticks upon a duck as being probably a more favourable host. About 25 females promptly attached themselves when placed upon the bare skin beneath the bird's wing, but all of them were dead and brittle by the fifth day, including a female which had become partially gorged. Thinking that the death of the ticks might be due to the dry heat in proximity to the bird's body, I bathed the bird periodically in sea-water to simulate the conditions of the marine birds (guillemots, ducks, gulls, etc.) upon which the tick is found in nature, but the results were negative both when fertilized and unfertilized ticks were used. Although 13 females were placed upon a young gull (*Larus ridibundus*), none of them survived upon the host. Females were also tried upon a canary, but with negative results. Curiously enough, a single female which somehow had managed to escape, attached itself

to the skin of my leg where it remained and partially gorged itself during a period of a week when it dropped off of its own accord. A note on the effect of this tick's bite is appended to this section.

Nymphs. 13 unfed nymphs were placed upon a duck, 12 on the gull and 12 on a young sparrow and canary. A few of them attached themselves to the duck, but all of these died *in situ* like the females.

Larvae. Unfed larvae which hatched out in the laboratory, although lively, refused to remain upon any of the hosts upon which they were tried.

Since our efforts to raise the tick under experimental conditions gave negative results it is impossible to make any statements with

Time required for metamorphosis.

Egg to Larva. The time being calculated from the date on which the first eggs were laid to the date when the first larvae appeared. The data here tabulated are based on the offspring of the females of Lot 1703 and each batch of eggs bears the maternal number. Eggs maintained at 12° C. during metamorphosis.

Eggs of ♀ Tick No.	Eggs laid on	Larvae emerged	Time in days
1	3. VIII. 1912	18. XI. 1912	107
2	19. VII.	11. X.	84
3	10. VIII.	7. XI.	89
4	24. VII.	21. X.	89
5	27. VII.	5. XI.	101
7	3. VIII.	18. XI.	107
9	27. VII.	21. X.	86
11	9. VIII.	30. XI.	113
12	25. VII.	23. X.	90
15	30. VII.	5. XI.	98
16	20. VII.	21. X.	93
17	27. VII.	7. XI.	103
18	16. VII.	9. X.	85
19	29. VII.	30. X.	93
20	29. VII.	30. X.	93
23	27. VII.	23. X.	88
25	29. VII.	5. XI.	99
26	24. VII.	18. X.	86
27	12. VII.	21. X.	101
28	3. VIII.	7. XI.	96
30	9. VII.	15. XI.	129

Larva to Nymph. From 51 gorged larvae (Lot 1307), collected on 2. VII. 1911, the nymphs emerged 4–17 days after the date of collection, at 12° C.

Nymph to Adult. From 31 gorged nymphs (Lot 1307), collected on 2. VII. 1911, the adults emerged 6–39 days after the date of collection, at 12° C.

regard to the time the tick remains upon the host during its different stages. It is clear, however, that it seeks a host three times, *i.e.* as a larva, nymph and adult female.

From the foregoing data regarding the time required for metamorphosis we may conclude that the larva developes in 84–129 days at an average temperature of 12° C.; eight lots of larvae emerged after 84–90 days, six after 93–99 days, six after 101–129 days. The data regarding the later stages do not permit of definite conclusions because the gorged larvae and nymphs were doubtless in a more or less advanced stage of metamorphosis when they were captured. Most of them were however quite lively, behaving like ticks which had but recently abandoned the host. It is possible therefore, if we take the longest periods observed, that metamorphosis from larva to nymph may take place in 17 days or more and that the nymph developes into an adult in 39 days or more. In the protocols dealing with the longevity of unfed adults (p. 84) I have noted the time required by each tick to undergo metamorphosis. It is worth mentioning that the males appear to require more time for metamorphosis than do the females, thus the longest periods noted for three males were 30, 34 and 39 days respectively, whereas the corresponding periods for three females were 19, 22 and 22 days respectively. That males may take longer than females to develope from gorged nymphs is rendered still more probable by the difference in size which I have noted between the gorged nymphs which give rise to males and females respectively.

Male and female nymphs.

Except by examining the internal organs, it has hitherto been found impossible to distinguish the sexes in the nymphs of Ixodidae. Having become convinced that the males of certain species of *Ixodes* do not feed upon the host (*I. hexagonus, caledonicus, canisuga, putus,* etc.) I sought to discover if any differences could be detected between the sexes in the nymphal stages. Arguing, that if the male has to store up all the energy required for its sexual life prior to emerging as an adult I concluded that there might be a difference observable in *the size* of the nymphs whence the males and females emerge. According to this view the male nymphs should be larger than the females because the male would store more food than the female in the nymphal stage. Having 22 gorged nymphs of *I. putus* at my disposal last year, I rapidly separated them into two lots: 11 large ones and 11 small or

medium-sized ones. From the 11 large nymphs there emerged as many males, from the medium-sized or small nymphs there emerged eight females and three males. All the large nymphs therefore gave rise to males, thus confirming me in my view. The large gorged ♂ nymphs measure 3·7–4·4 mm. in length, the small gorged ♀ nymphs measure 3·0–3·6 mm. in length when alive. The majority of the ♂ nymphs measure 4 mm. or over, the majority of ♀ nymphs do not exceed 3·2 mm. in length.

The size of adult I. putus.

In *Ticks*, Part II., the length of the ♂ is given as 3·7 mm. and that of the ♀ as 3·3 mm., the measurements having been made upon a few specimens preserved in alcohol. From the large number which have since passed through my hands I am now able to give measurements which show that there is a certain variation in size. Five of each sex were picked out from about 60 of Lot 1307 as showing obvious variations. The dimensions given do not include the capitulum.

5 ♂ measured		5 ♀ measured		
Length	Width	Length	Width	Scutum length
3·5 mm.	2·5 mm.	3·0 mm.	2·0 mm.	1·2 mm.
3·5	2·3	2·6	1·8	1·5
3·7	2·5	2·5	1·6	1·2
3·3	2·6	3·1	2·1	1·5
3·5	2·7	3·0	2·0	1·2
The average ♂ measures 3·5 × 2·5 mm.		The average ♀ measures 3·0 × 2·0 mm. Scutum length 1·3 mm.		

Copulation.

The process of copulation has been repeatedly observed by me both under natural conditions and in the laboratory. At Worm's Head the males were found copulating with gorged females only, but as soon as unfed females were brought together with males they copulated. The process is identical with that observed in other *Ixodes*, the male introducing spermatophores into the vulva of the female by means of his mouth-parts. In one instance the sexes were separated whilst *in coitu* and the bulb of the flask-shaped spermatophore was seen protruding from the vulva. By gentle traction the spermatophore neck within the vulva was withdrawn without injury. It measured as follows: total length 1·1 mm. of which a little over 0·3 mm. goes to the bulb, the neck measured just under 0·1 mm. in width, the bulb 0·3 mm.

Males. Lot 1307, captured 2. VII. 1911, included numerous gorged nymphs from a proportion of which 17 males and 14 females issued, their date of emergence and longevity when unfed being recorded as follows:

	♂ No.	Time which elapsed between day of collection and emergence	Tick survived for	Remarks
Lot 1307	1	7 days	12 days	Maintained at an average room temperature of 12° C. in corked tubes on moist filter paper, in semi-darkness.
	2	11	19	
	3	34	34	
	4	10	97	
	5	39	145	
	6	11	173	
	7	10	219	
	8	10	246	
	9	30	258	
	10	17	271	
	11, 12	4	327	
	13	11	345	
	14, 15	7	349	
	16	12	357	
	17	11	376	
Females.				
	♀ No.			
Lot 1307	1	6 days	58 days	Ditto.
	2	11	62	
	3	9	74	
	4	16	83	
	5	9	87	
	6, 7	4	134	
	8	9	175	
	9	6	178	
	10	22	191	
	11, 12	11	202	
	13	19	209	
	14	22	289	

Note:—Some males and females of Lot 1703 are still alive after 260 days (21. III. 13). Eleven unfed females out of 30 survived for 103 to 140 days.

Effect of the bite of I. putus.

When handling lot 1703, an unfed ♀ escaped, in spite of the usual precautions, and the next day (13. VII. 1912) was found attached on my left knee. On the 17th the spot itched slightly and appeared reddened around the seat of the puncture; the tick measured 3·5 mm. in length. The irritation then subsided and a pledget of lint, held in place by strapping, was then placed upon the spot. On the morning of the 20th the tick dropped off, having attained a length of 5·5 mm.; it

died two weeks later. The wound was but slightly noticeable, but a considerable amount of clear serum exuded from the puncture. On the 21st the puncture appeared patulous, reddened, and a circular area of oedema, about 3 cm. across, surrounded the bite, the skin itching over a surface extending about 7 cm. around the puncture. The itching continued, and on the 23rd an area of 4 cm. appeared swollen, darkly reddened and hard about a small central scab, the subcutaneous tissues being oedematous. This condition persisted for a couple of days, after which the swelling gradually subsided, an erythematous eruption appeared about the puncture, and there was a good deal of itching occasionally. The lint was now removed. As the slight eruption subsided, the skin about the bite began to scale all over a circular area 5 cm. in diameter, and, as the skin grew paler, it appeared yellowish-brown as if it had been bruised. Evidently there had been an extravasation of blood beneath the skin covering the part where peeling occurred. The central puncture appeared dark red. On 9th August the skin was yellowish, still peeling, however, and occasionally itching; the central puncture, covered by a scab measuring 2 mm. in diameter, was surrounded by thickened indurated tissue. On 18th August the skin surface appeared normal, still discoloured beneath; seat of puncture healing. On 19th, 20th and 22nd August the spot itched periodically; a slight fresh erythematous eruption appears, which has almost disappeared on 1st September, when there is still occasional itching; the seat of puncture red, nodular, the small scab came off exposing a small round, shallow ulcer 1·5 mm. broad. On 18. I. 1913 there is still a nodule at seat of bite; outwardly healed; slight discolouration (yellowish) about the size of a two shilling piece beneath the skin. The spot has itched violently several times for a few minutes since January 1. 20. III. 1913: the area about the seat of the puncture still appears slightly discoloured, and the small nodule itches violently for a few minutes about twice a week, the itching subsiding after a little rubbing with pressure.

Summary.

Ixodes putus has to feed three times upon a host, *i.e.* as a larva, nymph and adult. It has proved impossible to raise it upon animals under experimental conditions, consequently we do not know how long the different stages remain upon the host. The males do not attach themselves to the host, they remain in the vicinity of the nests of the birds upon which they fed as nymphs and when they emerge

from the nymphal skin they copulate with the gorged females which abandon the birds in the nest. The gorged nymphs from which the males issue are larger than those whence the females emerge. The time required for metamorphosis from egg to larva ranges between 84 and 129 days at 12° C., the nymphs may emerge after 17 days or more, the females after 22 days and the males after 34–39 days. Larvae have survived unfed for over 163 days, unfed nymphs for over 260 days, males have lived up to 376 days and females up to 289 days; all stages during the periods stated being confined in corked tubes in a moist atmosphere at room temperature. Oviposition commenced 4–36 days after the gorged females were collected in the birds' nests; about 25 days would appear to be the usual period preceding oviposition. The female continues to lay for 6–39 days, during which period she lays a comparatively small number of eggs, viz. 230–380 as was to be expected according to the theory advanced by me regarding the *Ixodes* which are parasitic on hosts with relatively fixed habitats[1]. The female, after she has finished ovipositing, may survive for 0–41 days, she usually dies, however, within four days.

The colouration in life and the changes in colour after death are different from anything hitherto observed in ticks, and it would be of interest to discover the reason for these colour changes. For notes on the variation in size, the process of copulation and the effect of the bite on man the reader is referred to the preceding pages.

IXODES CANISUGA[2].

The following notes relate to two lots (N. 1303 and 1304) of this species: Lot (*a*) comprised four replete females, one *in copula*, collected by me in sandmartins' nests at Boyton Hall Farm, Suffolk, 11. VII. 1911; they were found together with numerous other adults, nymphs and larvae infesting the young birds, gorged ticks and males being found within the nests. Lot (*b*) comprised 26 replete females and 24 males, collected by Mr R. F. L. Burton from sandmartins' nests at Longner Hall, Shrewsbury, 29. VII. 1911; these ticks reached Cambridge the day following. The females of both lots were isolated in corked tubes containing slightly dampened filter paper, the tubed ticks being maintained at room temperature in the laboratory.

[1] This *Journal*, IV. 46 (1911).

[2] The little that was hitherto known about the biology of this species is recorded in *Ticks*, Part II. pp. 316–317, wherein Wheler's observations are quoted.

Copulation was repeatedly observed *in vitro*. Several males copulated with females which had commenced to oviposit. By removing the male in some instances the spermatophore was discovered partially introduced into the vulva and the parts about the vulva were seen to be bathed with secretion. In short the process of copulation takes place as in other species of *Ixodes*.

Observations relating to oviposition.

	♀ No.	Number of days which elapsed before oviposition began	Number of days ♀ survived after oviposition began*	Number of eggs laid by female	
Lot *a*	1	4	33	—	Maintained at an average temperature of 23° C.
	2	3	28	—	
	3	3	28	—	
	4	5	—	598	
Lot *b*	1	8	28	624	Maintained at an average temperature of 19° C.
	2	6	16	450	
	3†	8	34	530	
	4	6	11	528	
	5†	7	29	546	
	6†	5	19	602	
	7†	5	21	830	
	8	5	30	624	
	9	5	31	530	
	10†	9	25	784	
	11†	5	13	594	
	12†	5	14	630	
	13†	5	19	588	
	14	5	20	—	
	15	6	15	—	
	16†	9	33	—	
	17	5	38	—	
	18	5	26	—	
	19	5	40	—	
	20†	9	34	—	
	21	6	17	—	
	22	6	30	—	
	23†	5	24	—	
	24	5	27	—	
	25	4	26	—	

* The death of the female usually taking place within 0–6 days of oviposition ceasing.

† Females observed to copulate on fifth day after collection when placed with males.

Time required for metamorphosis.

Egg to Larva. The time being reckoned from the date on which the female began ovipositing to the day on which the first larvae hatched. These eggs were laid by the females to which the foregoing record relates. They were maintained at a temperature of 19–23° C.

	Progeny of ♀ No.	Eggs laid on	Larvae emerged after
Lot *a*	1	15. VII. 1911	37 days
	2	14. ,,	32
	3	14. ,,	32
	4	16. ,,	32
Lot *b*	1	6. VI. 1911	38 days
	2	4. ,,	39
	3	6. ,,	37
	5	5. ,,	49
	6	3. ,,	40
	7	3. ,,	30
	8	3. ,,	39
	9	3. ,,	39
	10	7. ,,	39
	13	3. ,,	37
	14	3. ,,	30
	15	4. ,,	43
	16	7. ,,	34
	17	3. ,,	38
	18	3. ,,	36
	19	3. ,,	41
	20	7. ,,	34
	21	4. ,,	45
	22	4. ,,	31
	23	3. ,,	30
	24	3. ,,	30
	25	2. ,,	33

Longevity of larvae and males.

Larvae, the progeny of the females referred to in the protocol on p. 82, were kept in the corked tubes in which they hatched in August (Lot *a*) and July 1911 (Lot *b*) respectively. Maintained in cork tubes with dampened filter paper at an average temperature of 12° C.

	Progeny of ♀ No.	Larvae survived unfed for
Lot *a*	1	321 days
	2	346
	3	348
	4	319
Lot *b*	1	168
	2	321 <
	5	287
	6	294
	8	293
	15	291
	16	312
	18	311
	19	291
	21	145
	25	316

Males captured at the same time as the females were placed with them in separate tubes. Of the 4 males in Lot *a*, 2 survived for 22 and 33 days respectively. Lot *b* included 24 males of which 16 survived a sojourn of 5 days with the females with which they copulated. These males were separated from the females and placed in corked tubes at laboratory room temperature. They survived as follows:

2	lived	for	6 days	2	lived	for	29 days
1	,,		9 ,,	1	,,		33 ,,
1	,,		10 ,,	1	,,		38 ,,
2	,,		13 ,,	1	,,		47 ,,
1	,,		15 ,,	2	,,		56 ,,
1	,,		17 ,,	1	,,		123 ,,

Summary.

Owing to repeated failures at raising *Ixodes canisuga* upon laboratory animals (birds and mammals) the life history of this species was not completely followed. In common with other species of *Ixodes* whose life histories we know, it requires three hosts upon which to feed in the larval, nymphal, and adult stages. There is no evidence that the males feed upon the host for they have never been found upon the latter. Copulation occurs in the nests of the sandmartins, the process being similar to that observed in other *Ixodes*. Oviposition takes place

5–9 days after the replete female abandons the host in summer and the process lasts 11–40 days at 15–19° C., during which time the female lays 450 to 830 eggs, the average number being 600. The small number of eggs laid is in accordance with what I expected, that *Ixodes* parasitic upon hosts with fixed habitats lay fewer eggs since they are less exposed to loss of life than species occurring upon wandering hosts. The time required for metamorphosis from the egg to the larval stage is 30–49 days at 15–19° C. The larva may survive unfed for 348 days and males live up to 123 days in a corked bottle at room temperature in the presence of a slight degree of moisture. The longevity of unfed nymphs and females remains to be determined as well as the period which the different stages remain upon the host.

IXODES HEXAGONUS.

Observations made on nymphs and females etc. obtained 13. III. 1911 from a ferret in Cambridge.

Time required for metamorphosis.

Egg to Larva. Data relating to the progeny of the two females whose records follow. The time is reckoned from the date on which the female began ovipositing to the day on which the first larvae emerged.

Progeny of ♀ No.	Eggs laid on	Larvae emerged on	Time in days
1	27. IV. 1911	9. VII. 1911	73 at 13–18·5° C
2	21. IV. 1911	1. VIII. 1911	102 ,,

Larva to Nymph. No observations recorded as repeated efforts to raise these and other lots of larvae on hedgehogs and other ordinary hosts failed.

Nymph to Adult.

	Collected gorged on	Adults emerged on	Time in days
2 Nymphs	13. III. 1911	29. V. 1911 (2 ♀'s)	77 at 13–18·5° C.

Longevity of unfed females.

The two females which emerged from the foregoing nymphs were placed in a wooden pill-box on slightly dampened earth. The one lived for 9 days, the other over 42 days (18. X. 1911) at av. of 15° C.

Observations relating to oviposition.

♀ No.	Date when dropped from ferret	Began to oviposit after	Oviposition lasted	Female survived after oviposition ended	No. of eggs laid	Temperature at which ticks were maintained
1	13. III. 1911	45 days	32 days	6 days	650	av. 9° C.
2	,,	39 days	—	—	250	,,

Summary.

Attempts to raise *Ixodes hexagonus* upon their natural hosts in captivity have hitherto failed. From what we have observed we know that the tick requires three hosts upon which to feed, in the larval, nymphal and adult stages respectively. There is no evidence that the male ever sucks blood[1]. Oviposition takes place in 8–14 days after the female abandons the host in the spring and the process lasts 32 days at 9·5° C., the female may survive about a week after oviposition has ended. The female may lay 250 to 650 eggs, a comparatively small number, the tick being usually found on burrowing animals[1]. The time required for metamorphosis from the egg to the larval stage varied between 73 and 102 days and the corresponding period for the change from nymph and adult was 77 days at 13–18·5° C. An unfed female survived for 142 days at a temperature of 66° C. when confined in a pill-box. Unfed larvae survived at least three months.

IXODES RICINUS.

In *Ticks*, Part II. pp. 296–315, besides reporting original observations, I summarized what was known regarding the biology of this species. The following records give information of a somewhat more exact character in respect to several matters:

Time the tick remains upon the host.

Host	No. of Lot	Date when put on host	Host maintained at a temp. of	Number of gorged ticks collected on successive days	Remarks
Larvae.					
Calf	1308	3. x. 1911	16° C.	270 on day 4	Progeny of ticks from Ireland.
				30 ,, 6	Larvae had fasted 86–93 days before being put on calf.
,,	1308	10. x. 1911	16° C.	3 on day 3	Ditto.
				2 ,, 4	
				12 ,, 5	
				190 ,, 6–7	
				179 ,, 8	
				40 ,, 9	
				45 ,, 10	
Nymphs.					
Ram	1560	7.III.1912	6° C.	4 on day 3	Ticks from Tregothnan, Cornwall.
				7 ,, 4	
				1 ,, 6	
Adults.					
Ram	1560	7.III.1912	6° C.	1 on day 4	Ditto.
				2 ,, 5	
				1 ,, 7	

[1] Regarding the habits of the male see my earlier paper in *Parasitology*, IV. p. 67.

Time required for metamorphosis.

Egg to Larva: reckoned from the beginning of oviposition to the date when the first larvae issued from batches of eggs laid by isolated females:

Lot 1308 from Ireland Progeny of ♀ No.	Eggs laid on	Larvae emerged after	Mother-tick and eggs maintained at a temperature of
1	13. v. 1911	53 days	20° C.
2	14. ,,	56	,,
3	18. ,,	52	,,
4	18. ,,	54	,,
5	18. ,,	54	,,
6	19. ,,	51	,,
7	18. ,,	54	,,
8	18. ,,	49	,,
9	18. ,,	52	,,
10	18. ,,	54	,,
11	18. ,,	54	,,
12	18. ,,	62	,,
13	25. ,,	51	,,
Lot 417 1 ♀ received 23. v. 1908 from Scotland	13. vi. 1908	58	,,

Note:—Two to three days after the larvae emerged their hard chitinized parts appeared dark, and they had scattered themselves away from the exuviae, sometimes four days to a week elapsed before all the larvae had issued, reckoned from the first emergences in the one batch of eggs.

Larva to Nymph. Lot 1308. Gorged larvae dropped from a calf on 7. x. 1911. They were maintained at 10° C. during metamorphosis and emerged on 8. ii. 1912, the period which elapsed being 124 days.

Observations relating to oviposition.

Recording (*a*) the time that elapses before the gorged and fecundated female begins to oviposit after removal from the host; (*b*) the time occupied in oviposition; (*c*) the time which the female may survive after oviposition has been completed; (*d*) the number of eggs laid by single females.

The following record relates to ticks received from Mr H. W. Percy, 28. iv. and 3. v. 1911, having been collected, immediately before they were sent, from cattle suffering from redwater (Piroplasmosis) in the vicinity of Athlone, Co. Galway, Ireland.

Lot 1308 No.	Date of collecting gorged females from host	No. of days elapsing before oviposition began	No. of days oviposition lasted	No. of days tick survived after oviposition ended	No. of eggs laid by tick	Temperature at which the mother ticks were maintained from time of receipt
1	26. IV. 1911	17	45	8	—	24° C.
2	,,	18	44	7	—	,,
3	1. V. 1911	17	32	8	—	,,
4	,,	17	32	7	—	,,
5	,,	17	43	5	—	,,
6	,,	18	43	10	—	,,
7	,,	17	40	8	—	,,
8	,,	17	41	8	2400	,,
9	,,	17	40	1	—	,,
10	,,	17	40	0	—	,,
11	,,	17	—	—	2400	,,
12	,,	17	—	—	3200	,,
13	,,	24	—	—	2600	,,

Longevity of larvae.

Larvae (Lot 417) which emerged 10. VIII. 1908, survived unfed in a corked bottle until after 2. II. 1909 = 176 days, at 12° C. They were lively when last examined.

Summary.

This summary merely relates to the observations on *Ixodes ricinus* recorded in this paper:

The larvae remained upon a calf for 4–10 days at 16° C., the nymphs remained upon a ram for 3–6 days and the adults (females) for 4–7 days at 6° C. The time required for metamorphosis from the egg to the larval stage was 49–62 days at 15–20° C., from larva to nymph 124 days at 10° C. Oviposition began 17–24 days after the replete and fertilized females abandoned the host, the process lasted 32–45 days at 19° C. and the females laid 2400–3200 eggs. Females may survive 0–10 days after oviposition has ceased. Unfed larvae survived and were lively after 176 days at 12° C. in a corked bottle.

The larvae (Lot 1308) were the progeny of gorged females removed from cattle suffering from redwater in Co. Galway, Ireland. When placed upon a clean calf in Cambridge they produced piroplasmosis due to *Piroplasma divergens.*

HAEMAPHYSALIS LEACHI.

Mr Charles P. Lounsbury, formerly Government Entomologist, Cape Colony, was the first to raise this tick experimentally and to demonstrate that it transmits canine piroplasmosis in Africa. The protocols of his experiments (1901, pp. 5–6; 1902, pp. 5–7; 1904, pp. 27–29) give

the main points in the life history of the tick. From his brief statements regarding the tick, the following data are abstracted:

H. leachi is a three-host tick. The larvae and nymphs may drop off gorged from the host as early as 48 hours after being put on. The female remains upon the host for nine days (minimum) to 12–15 days. The time required for metamorphosis from egg to larva is 30–46 days in summer and 80–110 days in winter; the nymph emerges from the larval skin in 10–12 days in summer; the adult emerges from the nymphal skin in 18–20 days in summer and 70–105 days in winter. A female laid 4200 eggs. The males remain upon the host for many weeks, they release their hold upon the skin of the host and seek the females. By using an incubator he hastened the process of metamorphosis so that he was able to raise three generations in a year. The tick abandons the dying host.

The following records relate (*a*) to ticks received in 1902–1906 from Mr Lounsbury, Cape Colony, S. Africa (they were used for infection of dogs with *Piroplasma canis*), and (*b*) to ticks received 23. III. 1912 from Mr R. E. Montgomery, Nairobi, B. E. Africa. The last named were the progeny (larval stage) of two replete females collected beneath a box in which a jackal had been kept. The first and second generations raised in the laboratory are numbered respectively 1737 I and 1737 II.

The time the tick remains upon the host.

Host	No. of Lot	Date when put on host	Host maintained at a temperature of	Number of gorged ticks collected on succeeding days	Remarks
Larvae.					
Hedgehog	10	10. x. 1905	10° C.	126 on day 4 250 ,, 5	—
,,	11	18. x. 1905	9° C.	104 ,, 5 6 ,, 6	—
,,	12	28. x. 1905	9° C.	6 ,, 6	—
,,	...	16. xi. 1906	—	19 ,, 4 17 ,, 5 6 ,, 6 7 ,, 7 4 ,, 8 8 ,, 9–10 3 ,, 11	—
Jackal	1737 "I"	24. iii. 1912	18° C.	1 ,, 3 64 ,, 4 500 ,, 5 350 ,, 6 36 ,, 7	—

Host	No. of Lot	Date when put on host	Host maintained at a temperature of	Number of gorged ticks collected on succeeding days	Remarks
Larvae					
Dog	1737 "II"	22. xi. 1912	20° C.	44 on day 3 375 ,, 4 36 ,, 5	Larvae put on host 88 days (at 17° C.) after ecdysis. Progeny of 1737 I, ♀ 11.
Nymphs.					
Hedgehog	10	25. iv. 1906	10° C.	20 ,, 5	50 put on, 20 recovered.
,,	11	14. v. 1906	11° C.	3 ,, 3 12 ,, 5 2 ,, 7	30 put on, 17 recovered.
,,	13	4. vi. 1906	16° C.	4 ,, 5	20 put on, 4 recovered.
Jackal	1737 "I"	11. v. 1912	23° C.	13 by day 7	13 nymphs put on host 15 days after ecdysis; all recovered.
,,	,,	19. v. 1912	23° C.	24 on day 4 81 ,, 5 48 ,, 6 19 ,, 7 6 ,, 9 3 ,, 11	Nymphs put on host 23 days after ecdysis.
,,	,,	27. v. 1912	22° C.	12 ,, 3 51 ,, 4 5 ,, 5 3 ,, 7 7 ,, 9	Nymphs put on host 31 days after ecdysis.
Adults. (Female.)					
Dog	1	29. v. 1902	Room temp.	— ,, 12–15	—
,,	2	4. vi. ,,	,,	— ,, 11–12	—
,,	3	18. i. 1904	,,	— ,, 11	—
,,	4	26. i. ,,	,,	— ,, 14	—
,,	5	21. x. ,,	10° C.	— ,, 12–13	—
,,	6	22. x. ,,	10° C.	— ,, 14	—
Jackal	1737 "I"	3. vii. 1912	20° C.	2 ,, 10 1 ,, 12 2 ,, 14 1 ,, 16	Adults (7 ♂, 7 ♀) put on host 32 days after ecdysis; 6 ♀'s recovered.
,,	1737 "I"	15. vii. 1912	20° C.	5 ,, 8 5 ,, 9 18 ,, 10 10 ,, 11 7 ,, 12 1 ,, 13 1 ,, 14 1 ,, 16	Adults (about 100 ♂ and ♀) put on host 44 days after ecdysis; 48 ♀'s recovered.

The time required for metamorphosis.

The time required for metamorphosis is reckoned as follows:—(1) *Egg to Larva:* from the date on which the female began ovipositing to the day on which the first larvae emerged from the egg-shells; (2) *Larva to Nymph:* from the date on which the larvae dropped off gorged to the day on which the first nymphs emerged; (3) *Nymph to Adult:* from the date on which the nymphs dropped off gorged to the day on which the first adults emerged.

Egg to Larva.

Lot	Eggs laid on	Larvae emerged after	Eggs maintained at
1	15. XII. 1903	63 days	—
2	14. III. 1904	80	12° C.
3	2. V. 1904	58	13° C.
1737 I	16. VII.–1. VIII. 1912	26–37	20° C. *

* See table relating to the progeny of 39 ♀'s, etc. p. 97.

Larva to Nymph.

Lot	Host	Date on which gorged larvae dropped off host	Nymphs emerged after	Ticks maintained throughout at
1*a*	Ferret	13. VII. 1904	30 days	17° C.
1*b*	Rabbit	10. ,,	33	,,
1*c*	Hedgehog	11. ,,	32	,,
1*d*	Kid	29. VI. 1904	44	,,
2	Dog	2. IX. 1904	35	11° C.
3	Hedgehog	23–24. X. 1905	39	10° C.
1737 I	Jackal	27–30. III. 1912	31	24–26° C.

Nymph to Adult.

			Adults emerged after	
1	Rabbit	25. VII. 1904	42 days	14° C.
2	Hedgehog	30. IV. 1906	70	14° C.
1737 I	Jackal	23. V. 1912	15–16	24–26° C.

Longevity of unfed ticks.

The longevity of the unfed tick is reckoned from the date of its emergence from the egg in the case of the larva, from the larval skin in the case of the nymph, from the nymphal skin in the case of the adult.

Larvae.

Lot	Date of emergence		Remarks
1	12. VIII. 1904	Still lively after 56 days at 13° C.	In jar on earth.
2	29. VI. 1904	Dead after 44 days at 17° C.	,, ,,
1737 I	12. VIII. 1912	Lively after 221 days at 12° C.	Progeny of 31 ♀'s all lively after 119–221 days, in corked tubes. (21. III. 13.)

Nymphs.

1737 I	7. XII. 1912	Lively after 61 days at 12° C.	Then raised to adults.

Adults. Received VII. 1903 from Cape Colony, survived ca. 210 days at room temperature, and when placed on a dog produced fatal infection with piroplasmosis.

Observations relating to oviposition, etc.

Lot No.	Date when gorged females dropped from host	Oviposition began after	Ticks maintained at temperature of
1	X. 1903	60 days	Cool room.
2	I.–III. 1904	47	,,
3	3. III. ,,	24	,,
4	24. V. ,,	18	16° C.
5–8	IV.–V. ,,	14	16–21° C.
1737 I	VII.–VIII. 1912	3–5	23° C. *

* This holds for 33 out of 35 ♀'s, the two remaining oviposited on days 9 and 12 respectively.

Special record relating to 39 *H. leachi* ♀*'s* (*Lot* 1737 I) *and their progeny.*

No. of Tick	Days tick stayed on host	Day when gorged ♀ began to oviposit, reckoned from when it dropped off host	Oviposition lasted for days	Days ♀ survived after oviposition ceased	No. of eggs each ♀ laid	Day larvae started to emerge, reckoned from day oviposition began
1	10	3	25	2	—	27
2	10	4	26	5	—	26
3	12	4	29	5	2982	29
4	14	5	29	6	3626	28
5	14	3	31	8	4575	30
6	16	4	28	13	3362	28
7	8	4	32	5	3660	30
8	8	5	26	8	3043	29
9	8	4	21	5	—	28
10	8	9	27	8	2400	32
11	8	4	21	0	—	30
12	9	4	26	7	4803	33
13	9	3	34	15	3815	32
14	9	4	17	1	—	30
15	9	5	24	9	3595	33
16	9	5	31	12	—	32
17	10	4	22	13	—	30
18	10	3	30	31	3763	30
19	10	3	24	5	—	29
20	10	3	29	7	4817	29
21	10	3	31	15	—	29
22	10	4	32	6	—	29
23	10	4	29	3	3811	29
24	10	4	29	2	—	30
25	10	3	30	3	—	30
26	10	4	29	3	3395	32
27	10	—	—	—	—	—
28	10	3	30	15	—	30
29	10	5	30	6	—	30
30	10	—	—	—	—	—
31	10	5	28	6	—	29
32	11	—	—	—	—	—
33	12	—	—	—	—	—
34	10	3	30	6	—	30
35	10	3	26	3	—	31
36	10	12	—	—	*	—
37	13	3	28	2	—	30
38	14	3	28	0	—	34
39	16	5	37	10	—	37
		16. VII.–1. VIII. 12 at 22·5° C.	10. VIII.–11. IX. 12 at 20° C.	at 20° C.		12. VIII.–11. IX. 12 at 20° C.

* Laid a few unfertilized eggs.

Summary.

Haemaphysalis leachi requires three hosts upon which to feed during its larval, nymphal and adult stages. It readily attaches itself to the host at each stage in about a week after ecdysis. It is easily reared under experimental conditions upon a number of different hosts (jackal, dog, ferret, hedgehog, goat, rabbit), and it appears to be immaterial upon which of these hosts it feeds. The larva and nymph remain attached to the host for 3–7 days (2–3 days, Lounsbury), occasionally longer; the females remain attached longer, *i.e.* 8–16 days. The males may remain upon the host for many weeks (according to Lounsbury). The temperature of the air within the limits observed (9–23° C.) appears to exert little or no influence upon the time the tick remains upon the host, the warmth emanating from the latter being doubtless sufficient to keep the ticks active. The time required for metamorphosis[1] is influenced by temperature, thus the larvae hatch after 26–37 days at 20° C., in 58 to 80 days at 12–13° C.; the nymphs emerge, as a rule, after 30 to 40 days; adults emerge after 15–16 days at 24–26° C., whereas they may only emerge after 42–70 days at 14° C. The longevity of the unfed tick is considerable when the conditions are favourable; in small corked bottles the larvae were still very active after 169 days, the nymphs after 52 days and the adults after about 210 days when maintained at about 12° C. When males and females are simultaneously placed upon the host they scatter, but the sexes are found attached in close proximity to each other after 2–3 days. Copulation must take place upon the host, though it has never been actually observed. (Lounsbury has seen males, which he had marked, detach themselves and reattach themselves close to females; a male may mate with more than one female.) I find that the males do not seek the females as do *Ixodes* when the sexes have been removed from the host. The time which elapses before oviposition commences, after the replete female abandons the host, is markedly influenced by temperature; thus, when females were placed at 23° C. they began to lay after 3–5 days, at 16–21° C. after 14–18 days, at lower temperatures after 24, 47 to 60 days. Whereas an occasional female dies as soon as oviposition has ended, others may survive for a few days or, in exceptional cases, for a month. The female lays from 2400 to 4800 eggs. *H. leachi* begins to abandon its host on the approach of death in a manner that neither Lounsbury nor myself have observed in other ticks.

[1] See note on Lounsbury's observations on p. 94.

In nature, this tick may doubtless run twice through its life cycle in a year. By the use of an incubator, as first shown by Lounsbury, this author succeeded in raising three generations in a year. Taking average figures from my protocols of ticks raised under favourable conditions, the cycle may be completed in 153 days, as follows:

	Time required, in days	
From the time egg is laid to emergence of larva	30	(Eggs at 20° C.)
Larva hardens	7	
Larva stays on host	5	
Metamorphosis: Larva to Nymph	31	(Larvae at 17° C.)
Nymph hardens	7	
Nymph stays on host	5	
Metamorphosis: Nymph to Adult	15	(Nymphs at 24° C.)
Adult hardens	7	
Adult ♀ stays on host	12	
Gorged ♀ drops from host and waits before laying	4	
From the time egg is laid to emergence of larva	30	(Eggs at 20° C.)
	153 days	

HAEMAPHYSALIS PUNCTATA.

The only authors who have occupied themselves with the biology of this species are the writer (1908) and Stockman (1911, pp. 23–32); a detailed study of the external anatomy has been published by Nuttall, Cooper and Robinson (1908). The hosts upon which the tick is found are listed in the last mentioned paper (p. 161). The species was first raised by me on hedgehogs, this animal having been found to serve as a host in nature. The rabbit was also used as a host. The tick occurs most commonly on sheep, and between 1902 and 1905 we received large numbers from Kent, especially from the districts surrounding Lydd and Canterbury. We have also received specimens found on goats and ferrets, but we have no record of its natural occurrence on cattle in England. It is interesting therefore that McFadyean and Stockman were able to transmit British redwater, due to *Piroplasma divergens*, to cattle by means of this tick, although it can but play a very unimportant part if any in transmitting the disease in Europe, *Ixodes ricinus* being certainly the chief vector. It was not until I visited the laboratory at Alperton that the authors just quoted knew the species of tick with which they were working.

Stockman raised *H. punctata* upon the scrotum and ears, using cattle and sheep as hosts, the usual method of placing bags about the scrotum and ears being employed to recover the ticks as they dropped from the host. None of Stockman's ticks were incubated during metamorphosis;

they were maintained in corked bottles and glass dishes in an unheated outhouse, moulds being avoided by keeping the ticks somewhat drier than under natural conditions. The results of his raising experiments are fully referred to and incorporated in the following pages, the author's name being given in all cases where he is cited. Stockman's records were somewhat confused and it was not always easy to extract the desired information from them.

Seasonal occurrence on hosts. The specimens which have reached us have been adults collected in April. According to Stockman, in Kent and Devon, engorged females are found on sheep in April–June, in October and occasionally at other times of the year; engorged nymphs were found in May and August. Judging from observations at the Alperton laboratory on material collected at various times in the field, the ticks not being incubated during metamorphosis, Stockman concludes that larvae which feed and moult up to May, nymphs which feed and moult up to July, and adult females which feed and oviposit up to August, are all derived from eggs hatched the previous year. The larvae which hatch out, feed, and moult from July onwards, the nymphs which feed and moult from August onwards, and the adults which feed from October onwards are presumably all derived from eggs of the same year. All eggs laid in February, May and June hatched in July and August. Stockman believes that in nature the different stages emerge and feed as follows: the larvae do so chiefly in July and August, the nymphs in August–October, the females in October–November, but all stages may hibernate (fed or unfed) and appear on hosts in the spring. The females oviposit mainly in the spring. Starting with eggs laid in the spring, the ticks, according to Stockman, probably pass the next winter as gorged nymphs, and feed as adults in April–May of the following year, the cycle presumably lasting about 290 days.

Further observations made in the field appear to me required before definite conclusions can be arrived at; until such observations are made Stockman's hypothesis, based almost purely on laboratory experience, can scarcely be accepted.

Conclusions from the following protocol regarding the time *H. punctata* remains upon the host:

Larvae placed upon a hedgehog in June–August, the host being maintained at 16–17° C., remain 3–11 days upon the host, the majority dropping off gorged after 4–7 days. In November–December, the temperature being 10–12° C., they remain upon the host 7–21 days,

The time the tick remains upon the host (personal observations).

No. of Lot	Host	Date when put on host	Host maintained at a temp. of	Number of gorged ticks collected on succeeding days	Remarks
Larvae.					
1	Hedgehog	12. VI. 1905	17° C.	18 on day 3 333 ,, 4 120 ,, 5–6 10 ,, 7	—
2	,,	15. VI. 1905	17° C.	10 ,, 4 151 ,, 5 707 ,, 6 330 ,, 7 78 ,, 8 61 ,, 9–10	—
3	,,	8. VIII. 1905	16° C.	36 ,, 4 477 ,, 5–6 142 ,, 7 66 ,, 8–9 40 ,, 10 15 ,, 11	—
4	,,	17. XI. 1905	10° C.	10 ,, 21	—
5	,,	28. XI. 1905	12° C.	21 ,, 13 30 ,, 15 18 ,, 16	—
6	,,	19. XII. 1905	12° C.	2 ,, 7 7 ,, 8–13 5 ,, 14–19	—
7	Rabbit	2. VI. 1905	17° C.	3 ,, 13 5 ,, 14 4 ,, 15	—
8	,,	6. VI. 1905	17° C.	116 ,, 7 119 ,, 8 30 ,, 9	—
Nymphs.					
1	Hedgehog	29. VII. 1905	20° C.	152 by day 12	—
2	,,	3. XII. 1905	12° C.	33 ,, 25–27	—
3	,,	19. XII. 1905	12° C.	4 on day 13 1 ,, 14 1 ,, 20	(34 lost).
4	,,	22. I. 1906	8° C.	1 ,, 32 1 ,, 33	(22 lost).
5	,,	17. III. 1906	11° C.	7 ,, 11 11 ,, 12 4 ,, 13 4 ,, 14–17 8 ,, 18–20 11 ,, 21–29	(5 lost).
6	,,	11. IV. 1906	12° C.	7 ,, 9	(33 lost).
7	,,	14. V. 1906	13° C.	3 ,, 7 10 ,, 8 4 ,, 9	(13 lost).
Adults (♀).					
1	Hedgehog	9–11. IX. 1905	12° C.	1 ,, 14 1 ,, 17 3 ,, 18	Put on with males, none lost.

the majority dropping off gorged after 13–21 days. When placed on rabbits in June, at 17° C. they drop off gorged after 7–15 days.

Nymphs, placed on hedgehogs at 20° C., all dropped off by day 12; at 11–13° C. they dropped off after 7–29 days; at 8° C. after 32–33 days.

Adults (♀) remained upon the hedgehog at 12° C. for 14–18 days.

Note:—Stockman (1911), who raised *H. punctata* on cattle and sheep, records that,

	Remain on host	Average period
Larvae	4—12 days	5— 9 days
Nymphs	4—17	4—13
Adults	6—30	9—22

The time required for metamorphosis.

In the protocols dealing with this section I include those of Stockman with my own:

Egg to Larva.

Observer	No.	Date when first eggs were laid	Date when first larvae appeared	Time required for metamorphosis (days)	Temperature	Remarks
Nuttall	1	4. IV. 1905	25. VI. 1905	82	14° C.	——
Stockman	16/3	20. V. 1907	2. VIII. 1907	74	—	——
,,	—	—	—	38	—	The shortest time observed.

Larva to Nymph.

Observer	No.	Date when larvae gorged on host	Date when nymphs emerged	Time required for metamorphosis (days)	Temperature	Remarks
Nuttall	1	26. XII. 1905	8. V. 1906	159	10° C.	Host: hedgehog.
,,	2	1. I. 1906	2. VI. 1906	153	10° C.	,, ,,
Stockman	53	30. VII. 1907	15. III. 1908	197	—	Hibernation at outside temperature.
,,	32	30. VIII. 1907	29. IV. 1908	242	—	
,,	33	30. VIII. 1907	30. IV. 1908	243	—	
,,	—	—	—	14	—	The shortest time observed; the average time stated to be 16–29 days.

Nymph to Adult.

Observer	No.	Date when nymphs gorged on host	Date when adults emerged	Time required for metamorphosis (days)	Temperature	Remarks
Nuttall	1	10. VIII. 1905	28. VIII. 1905	18	At room temp., then at 30° C. during last 3 days	Host: hedgehog.
,,	2	8. XII. 1905	13. I. 1906	36	—	Host: dog.
,,	3	1. I. 1906	17. IV. 1906	107	9° C.	Host: hedgehog.
,,	4	28. III. 1906	14. IV. 1906	17–26	At room temp., then at 30° C. during last 14 days	,, ,,
Stockman	26	27. IX. 1907	23. VII. 1908	229	—	Hibernation at outside temp., a number survived winter but died without moulting.
,,	27	30. III. 1908	15. IV. 1908	15	—	——
,,	—	—	—	7	—	The shortest time observed.

Longevity of unfed ticks.

The following protocols include Stockman's observations as well as my own, the latter being but few:

Larvae.

Observer	No.	Date when emerged from eggs	Date to which larvae survived	Longevity unfed (days)	Remarks
Stockman	16/3	2. VIII. 1907	1. VI. 1908	303	This being the maximum period in 1 out of 9 lots.

Nymphs.

Observer	No.	Date of emergence	Date to which nymphs survived	Longevity unfed (days)	Remarks
Nuttall	1	3. VI. 1906	25. IX. 1906	114	At 16° C. most of the lot were dead.
Stockman	30	20. X. 1907	11. III. 1908	142	Hibernated at outside temperature.
,,	27	29. IX. 1907	30. III. 1908	182	Ditto, and after starving 182 days raised to adults.
,,	53	16. X. 1907	1. V. 1908	197	Hibernated at outside temperature.
,,	32	12. X. 1907	30. IV. 1908	200	
,,	21	12. IX. 1907	3. IV. 1908	203	
,,	29	20. IX. 1907	30. V. 1908	252	

Adults.

Observer	No.	Date of emergence	Date to which adults survived	Longevity unfed (days)	Remarks
Nuttall	1	13. I. 1906	—	255	At 12° C. lived longer, death not noted.
,,	2	18. IV. 1906	—	160	,, ,, ,,
Stockman	16/4	6. IX. 1906	18. IV. 1907	224	At outside temp., feeble when state recorded.

Oviposition.

The manner in which the female *H. punctata* lays her eggs was illustrated by me in the Harben Lectures 1908, but I kept no records of the time it takes for the tick to oviposit and did not count the number of eggs laid by single females. Judging from memory a female would lay 3000–5000. When the opportunity arises I shall have enumerations made. Apart from this the only other observations recorded are those of Stockman which are likewise incomplete. He states that the shortest and longest times which elapsed before oviposition commenced were 10 and 211 days respectively, the female usually ovipositing 24–29 days after abandoning the host. Some gorged females (Lot 27) survived 216 days without ovipositing. He gives no

temperature records in his protocols; the only records with dates are the following:

Stockman No.	Female dropped from host	Eggs first laid on	Oviposition commenced after
16/3	12. xi. 1906	20. v. 1907	189 days
16/4	12. x. 1906	15. ii. 1907	124 ,,

Stockman does not state how long oviposition lasts, but he says that the process may be interrupted with the onset of cold weather and resumed when the weather is warm.

Summary.

Haemaphysalis punctata seeks a host three times, feeding thereon in the larval, nymphal and adult stages. It readily attaches itself to the host 4–12 days after each ecdysis and is readily reared under experimental conditions upon hedgehogs, rabbits, sheep, cattle and ferrets. The larvae usually remain upon the host 4–7 days, although they may remain attached anywhere from 3 to 19 days. The nymphs usually remain attached for about a week, but this period of attachment may range from 4 to 33 days. Adult females remain attached for 6 to 22 days, the longer stay upon the host is doubtless due to their waiting to be fertilized. Males and females both behave like those of *H. leachi*, *q.v.* My observations suggest that when a hedgehog (hibernating host) is maintained at a low temperature the larvae and nymphs remain somewhat longer upon the host than in warm weather. The time required for metamorphosis is governed by temperature being much prolonged by cold. The larvae may hatch from the egg after 38 days (Stockman's shortest time) to 82 days (at 14° C., Nuttall); the nymphs may emerge after 14 days (Stockman's minimum) to 159 days (at 10° C., Nuttall) or after as long a period as 243 days (Stockman's maximum); the adults emerge after 7 to 229 days (Stockman's minimum and maximum); my observations show a range of 17 days (at 30° C.) to 107 days (at 9° C.). The longevity of the unfed tick is very marked; the records of Stockman and the writer show that larvae may survive for 303 days, nymphs for 252 days, adults 255 days; all stages are therefore able to hibernate readily in this condition. The time which elapses between the dropping of the gorged female from the host and the commencement of oviposition is markedly influenced by temperature, ranging accordingly from 10 to 211 days (Stockman). Data are lacking as to the duration of oviposition and the number of eggs laid by single females.

In nature, the tick will probably be able to complete its life cycle in a year but it may well run into two years in our climate. Taking average figures from the data recorded above, the cycle may be completed in 163 days[1], but the developmental period may of course be much prolonged:

	Time required in days
From the time egg is laid to emergence of larva ...	38
Larva hardens	7
Larva stays on host	6
Metamorphosis: Larva to Nymph...	14
Nymph hardens	7
Nymph stays on host	7
Metamorphosis: Nymph to Adult...	15
Adult hardens	7
Adult (♀) stays on host	14
Gorged ♀ having dropped off host, begins to lay after ...	10
From the time egg is laid to emergence of larva ...	38
	163 days

HYALOMMA AEGYPTIUM.

The only observations upon the biology of this common species appear to be those of Lounsbury (1900, p. 27; 1900, p. 44; 1904, p. 30) who reports that it attacks all farm animals in South Africa, doing most harm to sheep and goats and also troubling ostriches. Lounsbury's observations, as he himself states, are but fragmentary. He concluded that it is a three-host tick. He records the following observations:

> Both the larvae and nymphs leave the host to moult. Larvae remain upon the host for $3\frac{1}{2}$–$4\frac{1}{2}$ days. Males predominate on animals and remain a long time upon them. Females begin to oviposit 14 days after leaving the host (in February[2]) and the eggs are more resistant to dryness than those of *A. hebraeum* and *B. decoloratus*. The time required for metamorphosis from egg to larva varies; in four observations which are cited the times required were 37, 57, 63 and 79 days respectively; the longest period observed was six months.

The following observations were made by me in Cambridge, chiefly upon the progeny of four replete females (Lot 1305 *a*) which were

[1] Stockman gives a theoretically shortest cycle, but through an error in omitting to complete the cycle his period is too short.

[2] Southern hemisphere.

collected from sheep at Hammam-Meskoutine, Algeria, and sent to me 11. VI. 1911 by M. Paul Dechabert. These females oviposited after their arrival in Cambridge; one of them began to lay eggs 46 days after she had been taken from the host. My observations start with the larvae which were placed upon a host on 3–9. X. 1911, namely 32–38 days after they had hatched. Some incomplete records of earlier experiments are included in the protocols which follow; they relate to ticks (Lot X) which were collected from cattle in the vicinity of Rome and kindly sent to me 6. V. 1906 by Prof. Gosio from Italy.

Time the tick remains upon the host.

Larvae which dropped off the host *as gorged larvae.*

Host	No. of Lot 1305*a*	Date when put on host	Host maintained at a temp. of	No. of gorged larvae collected on successive days	Remarks
Ram	15	13. XI. 1912	4·5° C.	13 on day 8	Progeny of four females received from Algeria.
				20 ,, 9	
				16 ,, 10	
				10 ,, 11	
				1 ,, 12	
				1 ,, 13	
				1 ,, 14	
				62	
Hedgehog	5	29. VIII. 1912	16·5° C.	3 on day 6	Ditto.
				5 ,, 7	
				1 ,, 8	
				8 ,, 9	
				17	
Hedgehog	13	16. X. 1912	14° C.	6 on day 7	Ditto.
				45 ,, 8	
				152 ,, 9	
				8 ,, 10	
				4 ,, 11	
				149 ,, 12	
				247 ,, 13	
				117 ,, 14	
				82 ,, 15	
				810	
Guinea-pig	Y	12. VIII. 1912	17·5° C.	28 on day 9	Ditto.

Larvae which dropped off hedgehogs *as gorged nymphs*.

Host	No. of Lot	Date when put on host	Host maintained at a temp. of	No. of gorged nymphs collected on successive days	Remarks
Hedgehog	X	17. x. 1906	10° C.	1 on day 25	Progeny of females received 6. v. 1906 from Prof. Gosio, Rome.
				3 ,, 26	
				6 ,, 27	
				5 ,, 28	
				3 ,, 29	
				2 ,, 30	
				1 ,, 31	
				21	
Hedgehog	1305 13	16. x. 1912	14° C.	5 on day 32	Progeny of females received from Algeria.
				32 ,, 33	
				81 ,, 34	
				130 ,, 35	
				106 ,, 36	
				34 ,, 37	
				125 ,, 38	
				91 ,, 39	
				9 ,, 40	
				47 ,, 41	
				23 ,, 42	
				17 ,, 43	
				5 ,, 44	
				23 ,, 45–46	
				728	
Hedgehog	1305 5	29. VIII. 1912	14·5° C.	1 on day 35	
				3 ,, 39	
				1 ,, 40	
				1 ,, 41	
				6 ,, 42	
				12	

Nymphs which dropped off *unfed* from a hedgehog on 5. XI. 1912 were placed upon another hedgehog after the lapse of 78 days, the nymphs appearing lively: 1 gorged nymph dropped off the host on 7. II. 1913, the 16th day.

Adults placed on a calf 16. II. 1912. Females dropped off gorged and fecundated after 6–8 days. Adults placed on a calf 1–5. v. 1912. Females dropped off gorged and fecundated after 7–8 days, the host being maintained at a temperature of 16–19° C.

Time required for metamorphosis.

Egg to Larva.

Lot	First eggs laid on	First larvae emerged after	Temp. at which eggs were maintained	Remarks
X 1305	23. VI. 1906	44 days	16° C.	Italian ticks.
Progeny of ♀ No. 1	29. II. 1912	35 days	18° C.	Algerian ticks.
2	2. III.	44	,,	
3	29. II.	41	,,	
4	3. III.	39	,,	
5	4. III.	42	,,	
6	4. III.	40	,,	
7	2. III.	46	,,	
9	3. III.	49	,,	
12	4. III.	49	,,	
13	4. III.	39	,,	
14	5. III.	52	,,	
15	5. III.	46	,,	
16	4. III.	51	,,	
17	5. III.	49	,,	
18	4. III.	51	,,	
19	5. III.	49	,,	
20	9. III.	45	,,	
21	20. V.	45	19° C.	
22	20. V.	46	,,	
23	21. V.	48	,,	

Larva to Nymph. When gorged larvae drop off the host (metamorphosis off the host).

No. of Lot 1305*a*	Host	Gorged larvae first dropped off host on	Tick maintained at	Days which elapsed before nymphs emerged
15	Ram	21. XI. 1912	19° C.	16
5	Hedgehog	4. IX.	20° C.	20
13	Hedgehog	23. X.	21° C.	3–8*

* The shortness of the period apparently required for metamorphosis in this case may be attributable to gorged larvae dropping off the hedgehog after partial metamorphosis. The observation on the ram must, therefore, be accepted as more trustworthy.

When unfed nymphs drop off the host.

		Larvae put on host on	Unfed nymphs collected	
13	Hedgehog	16. X. 1912	25 on day 20	Hedgehog in a room at 13·5° C.
			19 ,, 21–23	
			17 ,, 24–26	
			16 ,, 27	
			4 ,, 28	
			2 ,, 29	

Nymph to Adult.

No. of Lot 1305*a*	Host	Gorged nymphs first dropped off host on	Ticks maintained at	Days which elapsed before adults emerged
—	Hedgehog	21. X. 1912	14° C.	95
5	,,	3. X.	18° C.	20
13	,,	17. XI.	37° C.	23–15

Notes in relation to oviposition of isolated ♀'s (Lot 1305) in pill-boxes.

♀ No.	Date when ♀ dropped off host	Days which elapsed before oviposition began	Days oviposition lasted	No. of days ♀ survived after oviposition ended	No. of eggs laid by each female	Temperature at which ♀'s were maintained
1	22. II. 1912	8	46	0	11930	15° C.
2	23. II.	8	38	0	10351	,,
3	24. II.	6	43	3	12499	,,
4	25. II.	7	43	19	14300	,,
5	,,	8	40	23	12747	,,
6	,,	8	45	1	11962	,,
7	,,	6	40	2	15510	,,
8	,,	8	45	26	—	,,
9	,,	7	40	3	12876	,,
12	26. II.	7	33	0	—	,,
13	,,	7	44	7	13940	,,
14	27. II.	7	43	0	12896	,,
15	,,	7	46	22	—	,,
16	,,	6	59	17	—	,,
17	,,	7	38	—	—	,,
18	,,	6	44	2	—	,,
19	,,	7	48	6	—	,,
20	29. II.	9	35	11	—	,,
21	8. V.	12	31	4	—	17–19° C.
22	9. V.	11	42	1	—	,,
23	13. V.	8	27	7	—	,,

Longevity of unfed larvae, nymphs and adults.

(Lot 1305.)

Larvae which emerged on 10. IV. 1912 were very lively on 21. III. 1913, *i.e.* after 345 days. (12 lots of larvae which emerged at about the same time were equally lively after 256 days and upwards; they were successfully raised. They were maintained at room temperature[1] in tightly corked tubes.)

Nymphs which abandoned the host in an unfed state on 7. XII. 1912 were very active after 52 days. Similar nymphs which dropped off the host on 31. X. 1912 were fairly active after 89 days (28. I. 13); they died after 141 days. (At room temperature[1] in tightly corked tubes.)

Adults which emerged 24. I. 1912 were lively after 369 days and some were still living after 421 days (21. III. 13). (At room temperature[1] on earth in jars.)

Summary.

The foregoing raising experiments show that *Hyalomma aegyptium* usually requires three hosts upon which to feed in its larval, nymphal and adult stages. When larvae are placed on hedgehogs, however, about half of them drop off as gorged nymphs, so that upon this host,

[1] Averaging 12° C.

contrary to what occurs when they are put on sheep, they behave like two-host ticks. This peculiar behaviour on hedgehogs is doubtless due merely to the gorged larvae remaining entangled amongst the host's spines. The larvae remain upon the host 6–15 days ($3\frac{1}{2}$ to $4\frac{1}{2}$ days according to Lounsbury) before they drop off gorged. When they drop off as gorged nymphs from hedgehogs they do so 25–46 days after the larvae are put on the host. Nymphs remain upon the host for about eight days. Females remained upon a calf 6–8 days. Males remain longer upon the host—I have seen camels in Biskra upon which only males could be found. The time required for metamorphosis from the egg to the larval stage is 35–51 days and from the larval to the nymphal stage the period required is 16–20 days. Nymphs change to adults in 95 days at 14° C. to 12–15 days at 37° C., metamorphosis, as is usual with ticks, being markedly accelerated by warmth. Oviposition commences 6–12 days after the gorged and fecundated female abandons the host; the process lasts 27–59 days, and during this period, the temperature being 15–19° C., a female lays 10350–15500 eggs. Two of the four females received from Algeria only laid 4300 and 4350 eggs respectively; this relatively small number is attributable to their having been removed from their host in Africa when they were incompletely gorged. The females survive for 0–26 days after oviposition has ended. Copulation must take place upon the host. Longevity is marked: larvae were lively after 345 days, nymphs after 89 days and adults after 369 days at room temperature; some adults lived over 421 days.

From the data given in my protocols, the shortest time required for the completion of the life cycle was 151 days, made up as follows:

	Time required in days	
From time egg is laid to emergence of larva ...	35	(Eggs at 18° C.)
Larva hardens	7	
Larva stays on host	6	
Metamorphosis: Larva to Nymph	16	(Larvae at 19° C.)
Nymph hardens	7	
Nymph stays on host	6	
Metamorphosis: Nymph to Adult	20	(Nymphs at 18° C.)
Adult hardens	7	
Adult ♀ stays on host	6	
Gorged ♀ drops off host and waits before laying ...	6	
From time egg is laid to emergence of larva ...	35	(Eggs at 18° C.)
	151 days	

RHIPICEPHALUS APPENDICULATUS.

The species was first raised by Lounsbury in South Africa in connection with investigations upon East Coast Fever in cattle during which he demonstrated that it is the usual vector of this devastating disease:

> Lounsbury (1904, pp. 3–7) has shown that *R. appendiculatus* is a three-host tick. The larvae stay upon the host 3–10 days or longer depending upon the more or less favourable seat of attachment upon the skin of the host; the nymphs gorge and abandon the host in a few days and the females remain attached for about nine days when put on the host simultaneously with males; the latter may remain for a considerable time upon the host. The tick prefers to attach itself to the inner surface or hairy margin of the ears of cattle which serve as its chief hosts. Metamorphosis from egg to larva takes place in five weeks to five months according to the temperature at which the eggs are maintained prior to hatching, cold therefore markedly retarding development. Larvae change to nymphs in two weeks or more. All stages may survive unfed for several week on grass and unfed nymphs survived for seven months in a corked bottle containing moist sand. Adults are scarce on cattle in winter and in the course of Lounsbury's experiments it was found difficult to make them attach themselves to cattle during the cold season. The contrary holds for nymphs and larvae which are found on cattle in winter and readily attack their hosts in cold weather. Several thousand eggs are laid by each female. Two generations at most are produced in a year.

In the course of my investigations on East Coast Fever I took occasion to make a systematic study of the biology of the tick of which I received several infected lots from South Africa, thanks to the kindness of Mr C. P. Lounsbury. My raising notes only relate however to Lot (*a*) received 10. xi. 1910 and Lot (*b*) received in 1905. We have maintained the strain of Lot (*a*) to date.

Time the tick remains upon the host.

Larvae.

Progeny of ♀ No.	Host	Date when put on host	Host maintained at a temperature of	Number of gorged larvae collected on succeeding days
Lot *a* 1	Calf	25. x. 1911	16° C.	16 on day 7
				20 ,, 8
				16 ,, 9
				42 ,, 10
				53 ,, 11
				27 ,, 12
				11 ,, 13
				40 ,, 14
				38 ,, 15
2	Calf	28. xi. 1911	16° C.	369 on day 5
				350 ,, 6
				80 ,, 7
3	Calf	4. v. 1912	—	313 on day 4
				160 ,, 5
5	Calf	15. iii. 1912	7° C.	14 on day 3
				219 ,, 4
				130 ,, 5
				42 ,, 6
9	Calf	16. ii. 1912	15° C.	95 on day 4
				12 ,, 5
18	Calf	29. x. 1912	11° C.	52 on day 4
				240 ,, 5
				60 ,, 6
20	Calf	24. vii. 1912	22° C.	27 on day 3
				1040 ,, 4
				176 ,, 5
				70 ,, 6
				45 ,, 7
23	Calf	28. xi. 1912	7° C.	12 on day 4
				53 ,, 5
				416 ,, 6
				224 ,, 7
				22 ,, 8
				6 ,, 9
Lot *b*	Hedgehog	23. iv. 1905	13° C.	— on days 5–11

Nymphs.

Progeny of ♀ No.	Host	Date when put on host	Host maintained at a temperature of	Number of gorged nymphs collected on succeeding days
Lot *a* 1	Calf	4. VII. 1912	20° C.	2 on day 6
3	Calf	24. X. 1912	11° C.	1 on day 7
				4 ,, 8
				12 ,, 9
				21 ,, 10
				11 ,, 11
5	Calf	11. VII. 1912	24° C.	1 on day 5
				8 ,, 6
				3 ,, 7
				1 ,, 8
20	Calf	7. X. 1912	14° C.	5 on day 7
				2 ,, 8
				3 ,, 9
				1 ,, 10
Lot *b* 1	Hedgehog	7. VI. 1905	16° C.	Dropped after 4–6 days
2	Hedgehog	26. V. 1905	18° C.	Dropped after 5–9 days

Adults (♀).

Lot *a* ♀ No.	Host	Date when put on host	Host maintained at a temp. of	Number of days ♀ stayed on host
1	Calf	19. V. 1911	15° C.	8
2	,,	19. V.	15	8
3	,,	19. V.	15	10
8	,,	3. VII.	24	6
9	,,	25. IV.	15	8
11	,,	9. XI.	16	11
12	,,	9. XI.	16	11
14	,,	9. XI.	16	14
17	,,	9. II. 1912	15	10
18	,,	9. II.	15	10
19	,,	9. II.	15	10
20	,,	9. II.	15	10
21	,,	9. II.	15	12
22	,,	29. II.	10	9
24	,,	29. II.	10	11
25	,,	29. II.	10	12
26	,,	6. VII.	24	9
27	,,	6. VII.	24	11

Time required for metamorphosis.

Egg to Larva.

Progeny of ♀ No.	Eggs laid on	First larvae emerged after	Maintained during metamorphosis at
Lot *a* 1	8. VI. 1911	65 days	19° C.
2	7. VI.	56	,,
3	8. VI.	59	,,
5	11. VI.	52	,,
8	19. VII.	48	17° C.
11	20. I. 1912	44	,,
12	20. I.	51	,,
14	12. I.	49	,,
17	29. II.	49	,,
18	28. II.	34	,,
19	27. II.	33	,,
20	28. II.	35	,,
21	1. III.	32	,,
22	15. III.	48	,,
23	18. III.	49	,,
24	18. III.	47	,,
25	18. III.	49	,,
26	23. VII.	45	,,

Larva to Nymph.

Progeny of ♀ No.	Gorged larvae dropped from host on	First nymphs emerged after	Maintained during metamorphosis at
Lot *b* 2–5	15–25. V. 1905	4–6 days	30° C.
Lot *a* 23	2. XII. 1912	10	21° C.
3	8. V.	13	18° C.
20	27. VII.	21	17° C.
5	18. III.	25	16° C.
9	20. II.	41	15° C.
1	1. XI. 1911	75	14° C.
8	24. XI.	60	13° C.

Nymph to Adult.

Progeny of ♀ No.	Gorged nymphs dropped from host on	First adults emerged after	Maintained during metamorphosis at
Lot *a* 3 *a*	4. XI. 1912	10 days	37° C.
3	31. X.–4. XI.	37	25° C.
5	16–20. VII.	28	20° C.
1	10. VII.	21	20° C.
20	13–17. X.	64	14° C.

Observations relating to oviposition.

Lot *a* ♀ No.	Date when ♀ dropped off calf or cow	Oviposition began after	Oviposition continued during	♀ survived after oviposition ended for	Number of eggs each ♀ laid	Temperature at which ♀ was maintained
1	27. v. 1911	12 days	56 days	3 days	—	19° C.
2	27. v.	11	40	0	3000	,,
3	29. v.	10	39	0	4160	,,
5	2. vi.	9	47	7	5770	,,
8	9. vii.	10	45	4	—	18° C.
9	3. v.	23	44	0	—	19° C.
11	20. xi.	61	39	2	4704	12° C.
12	20. xi.	61	38	3	5548	,,
14	23. xi.	50	45	13	4956	,,
17	19. ii. 1912	10	39	7	—	17° C.
18	19. ii.	9	19	4	3712	,,
19	19. ii.	8	15	7	4200	,,
20	19. ii.	9	19	0	4230	,,
21	21. ii.	9	18	8	3468	,,
22	9. iii.	6	31	—	—	,,
24	11. iii.	7	26	2	—	,,
25	12. iii.	6	27	5	—	,,
26	15. vii.	7	38	0	4543	,,
27	19. vii.	8	28	1	3648	,,

Besides the above 19 ♀'s of which an exact record was kept there were four which laid unfertilized eggs and three which died without ovipositing. The four which laid unfertilized eggs remained upon the host for 14, 15, 18 and 19 days respectively, which is longer than all but one of the 19 which laid fertile eggs. The three females which died without ovipositing remained upon the host for 11, 23 and 24 days respectively. The more prolonged stay of infertile females upon the host was probably due to their waiting for a male.

Longevity of unfed larvae, nymphs and adults.

Larvae.

Progeny of ♀ No.	Emerged from egg on	Number of days larvae lived unfed	Larvae maintained at a temp. averaging	
Lot *a* 1	12. VIII. 1911	75	14° C.	Afterwards fed on host and behaved normally.
2	4. VIII.	116	,,	
3	6. VIII.	273	12° C.	
5	2. VIII.	226	,,	
9	21. VII.	210	,,	
18	2. IV. 1912	210	,,	
20	3. IV.	119	14° C.	
23	6. V.	187	12° C.	
—	1. III.	333 (lively)	—	Not fed on host. In a feeble state after 385 days (21. III. 13).

Nymphs.

Progeny of ♀ No.	Emerged on	Alive or dead after (days)	Nymphs maintained at a temp. averaging	
Lot *a* 5	12. IV. 1912	90 (alive)	18° C.	Afterwards raised to adults. They behaved normally.
3	18. V.	159 ,,	16° C.	
1	19. I.	167 ,,	17° C.	
8	23. I.	175 (dead)	17° C.	
9	12. III.	247 ,,	16° C.	
—	17. VIII.	164 (lively)	—	Used for raising.

Adults.

Progeny of ♀ No.	Emerged on	Alive after (days)	Adults maintained at temp.
Lot *a* I	31. VII. 1912	181 (lively)	Of room.
II	25. VI. 1911	640 (some alive)	,,

Summary.

Rhipicephalus appendiculatus requires three hosts upon which to feed in its larval, nymphal and adult stages. The larvae remain upon the host 3–7 days in most cases; when they remain considerably longer they either do not imbibe blood freely or they may not actually attach themselves on the day on which they were placed on the host; gorged larvae have dropped off the host up to 15 days after the unfed larvae were placed on the host. Nymphs remained upon the host 5–11 days and fertilized replete females abandoned the host after 6–14 days. The males may stay on longer. Unfertilized females may remain upon the host up to 24 days. The temperature at which the host is maintained, within the limits observed, exerts no apparent influence upon the time that the different stages of the tick remain attached. Metamorphosis

takes place: from egg to larva in 32–65 days at 17–19° C.; from larva to nymph in 4–6 days at 30° C., in 21–41 days at 15–17° C., in 60–75 days at 13–14° C.; from nymph to adult in 10 days at 37° C., in 21–28 days at 20° C., in 64 days at 14° C. Temperature therefore markedly influences the rate of development. Oviposition commences 6–23 days at 17–19° C. to 50–61 days at 12° C. after the female abandons the host, the process lasting 15–56 days, during which period the female lays 3000–5770 eggs. Unfed larvae and nymphs were still lively after 333 days and 164 days respectively in a tightly corked bottle maintained at room temperature in a darkened cupboard in the laboratory. Unfed adults were lively after 181 days on moistened earth in a gauze covered jar kept in the cupboard; we have one lot of which a few individuals were living (unfed) after 630 days, a single male being still alive after 682 days (21. III. 13).

The minimum time required for this species to complete its life cycle, judged from the data contained in my protocols, would be about 147 days, as follows:

	Time required in days	
From time egg is laid to emergence of larva ...	32	(Eggs at 17–19° C.)
Larva hardens	7	
Larva stays on host	3	
Metamorphosis: Larva to Nymph ...	21	(Larvae at 17° C.)
Nymph hardens	7	
Nymph stays on host	5	
Metamorphosis: Nymph to Adult... ...	21	(Nymphs at 20° C.)
Adult hardens	7	
Adult ♀ stays on host	6	
Gorged ♀ drops off host and waits before laying	6	
From time egg is laid to emergence of larva ...	32	(Eggs at 17–19° C.)
	147 days	

In concluding this paper I have pleasure in acknowledging the very valuable aid I have received from my Laboratory Assistant, Mr B. G. Clarke, who has been indefatigable and conscientious to a degree in connection with all the details of the practical work of raising the ticks. The amount of labour and attention involved in raising ticks and keeping accurate protocols can only be grasped by those who have attempted it themselves. Were it not for Mr Clarke's enthusiasm for the work and his care in matters of detail I should not have been able to publish the results which are incorporated in this paper.

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This handbook gives a brief aecount of the prineipal insect and mite pests of erops in the Lesser Antilles. The author, who is entomologist on the Staff of the Dep't of Agrieulture, writes on the subject with authority. The object of the book is mainly edueational for agrieulturalists, and it should answer the purpose for which it is intended, being indeed a ereditable production. N.

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The book represents the subject matter of a course of leetures given by the author to students at the University of Bern. It contains three chapters dealing with (i) Stinging, biting and injurious or rash-indueing arthropods; (ii) Parasitie arthropods; (iii) Arthropods whieh transmit disease. The illustrations, mostly borrowed from other authors, are on the whole fair, though they have suffered in the process of reproduetion. The booklet can be recommended as an introduction and cursory review of the subjeets of whieh it treats. N.

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This is a remarkable and original book, well written and well illustrated, and full of information whieh eannot be found in more pretentious works. The author has disearded useless lumber and eonfines himself to what is useful to-day. It is a book that should be in every laboratory dealing with histology, zoology, botany and parasitology. We heartily eongratulate both author and publisher on its appearanee. N.

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LULHAM, R. (1913). *An Introduction to Zoology.* With directions for practical work (Invertebrates). London: Macmillan & Co., Ltd., St Martin's Street. 457 pp., 6 pls., 328 figs. 19 × 12 cm. Cloth. Price 7*s.* 6*d.*

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